GENERA ORCHIDACEARUM

Volume 2

Orchidoideae (Part one)

Edited by

Alec M. Pridgeon, Phillip J. Cribb,
Mark W. Chase, and Finn N. Rasmussen

For centuries orchids have been among the most popular of plant families, with thousands of species and hybrids cultivated the world over for the diversity, beauty, and intricacy of their flowers.

The aim of *Genera Orchidacearum* is to produce a robust and natural classification of the orchids, something which has eluded plant scientists and orchid enthusiasts for years. The editors, who are all distinguished orchid specialists, are incorporating the wealth of new molecular data into a truly phylogenetic classification and identifying the areas and taxa needing additional work. To this end, they have invited several international specialists to contribute in their particular areas of expertise. Each volume of this monographic series will provide comprehensive coverage of one or two orchid subfamilies. The series as a whole will be an indispensable reference tool for scientists and for orchid breeders, collectors, and growers.

Orchidaceae is the largest monocotyledon family and perhaps the largest plant family in the numbers of species it comprises (ca. 20,000), but for a variety of reasons it remains one of the least understood. The fossil record is poor, active research relatively scarce until recent years, both the size and geographical distribution of the family are huge, and its largely tropical distribution hinders access.

This second volume treats 101 genera in three of the seven recognized tribes of the subfamily Orchidoideae—Orchideae, Diurideae, and Diseae. Comprehensive descriptions are provided for each genus and subtribe which include the complete nomenclature, description, distribution, anatomy, palynology, cytogenetics, phytochemistry, phylogenetics, pollination, ecology and economic uses. Cultivation notes are included for those genera known to be in hobbyist collections. All genera are beautifully illustrated with many line drawings, maps and colour photographs. Volume Three will cover the remaining tribes of Orchidoideae and the subfamily Vanilloideae.

The Editors

Alec M. Pridgeon is Sainsbury Orchid Fellow at the Royal Botanic Gardens, Kew

Phillip J. Cribb is Deputy Keeper of the Herbarium and Curator of the Orchid Herbarium, Royal Botanic Gardens, Kew

Mark W. Chase is Head of the Molecular Systematics Section, Jodrell Laboratory, Royal Botanic Gardens, Kew

Finn N. Rasmussen is Associate Professor at the Botanical Institute, University of Copenhagen.

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Alec M. Pridgeon, Phillip J. Cribb,
Mark W. Chase
Royal Botanic Gardens, Kew

and

Finn N. Rasmussen
Botanical Laboratory, University of Copenhagen

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PREFACE

This volume of *Genera Orchidacearum* treats 101 genera in three of the seven tribes of subfamily Orchidoideae (including Spiranthoideae) now recognized—Orchideae, Diurideae, and Diseae—adding to the seven genera covered in Apostasioideae and Cypripedioideae in Volume 1. For each of the genera and/or their respective subtribes contributors have provided synonymy, derivation of name, description with illustrations, and distribution with maps as well as treatments reflecting the current state of knowledge of their anatomy, palynology, cytogenetics, phytochemistry, phylogenetics, ecology, pollination, and economic uses. Authorities for botanical binomials are provided at their first occurrence in the text. Cultivation notes are supplied for those genera known to be in hobbyist collections, with emphasis on their artificial propagation rather than collection from the wild. A glossary of terms is provided in Volume 1 of this series. Volume 3 will include the remaining tribes of Orchidoideae, subfamily Vanilloideae, and a glossary for both subfamilies. Later volumes will be devoted to Epidendroideae.

Numbers assigned to individual genera are based solely on order of their alphabetic appearance in the text solely as a convenience to the reader and bear no relation to phylogenetic relationships or level of evolutionary advancement, nor should they be construed as such. On the endpapers of this and future volumes is an alphabetic/numeric list of genera covered to date as an aid to finding generic treatments quickly within or among the various volumes.

Our generic and suprageneric concepts of orchids are changing rapidly with the almost exponential increase in nuclear and plastid DNA sequences combined with other types of evidence coming in from around the world. Although we have vast amounts of molecular data to reassess the monophyly and phylogenetics of many genera, there are gaps in coverage and insufficient information to revise the classification of other genera and higher taxa at this time. For instance, there is now preliminary evidence that Diseae *sensu* Dressler (1993) are a paraphyletic grade rather than a clade and that Coryciinae are not monophyletic if *Disperis* is maintained in Diseae. Pending additional ITS and plastid DNA sequences of Diseae, however, we have chosen the conservative approach and retained *Disperis* within Diseae, knowing that the classification will likely change before the final version in the last volume of this series. Another significant gap in our knowledge is the African membership of Orchideae (particularly the pantropical genus *Habenaria*), for which little material has been available for molecular studies. Here, too, taxonomic changes are likely in the years to come.

Reliance on chiefly molecular characters to define monophyletic groups and resolve orchid phylogeny makes artificial keys to tribes, subtribes, and genera using morphological characters difficult and even frustrating. Rates of molecular and morphological evolution are more congruent in some orchid groups (for example Cypripedioideae) than others (such as Oncidiinae). Morphological hypotheses are complicated by homoplasious floral adaptations to pollinators for example, so there is no reason to expect that we should be able to construct phylogenetic keys for identification purposes, much as we would like. Nevertheless, contributors to this volume have drafted artificial keys to the various taxa for publication here; readers should find the keys useful if not infallible.

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ALEC M. PRIDGEON
PHILLIP J. CRIBB
MARK W. CHASE
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CONTRIBUTORS

Abbreviations used in text for authorship credit:

CHRISTOPHER BAILES (CB)
RHS Garden Rosemoor, Great Torrington, North Devon EX38 8PH, UK

DR. RICHARD M. BATEMAN (RB)
Department of Botany, Natural History Museum, Cromwell Road, London SW7 5BD, UK

DR. COLIN BOWER (CCB)
PO BOX 300, Orange, New South Wales 2800, Australia

DR MARK W. CHASE (MWC)
Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK

DR MARK A. CLEMENTS (MAC)
Centre for Plant Biodiversity Research, Australian National Herbarium, CSIRO Plant Industry, GPO Box 1600, Canberra, ACT 2601, Australia

DR SALVATORE COZZOLINO (SC—ORCHIDEAE)
Dipartimento di Biologia Vegetal, Universitá di Napoli Federico II, via Foria 223, I–80139 Napoli, Italy

DR PHILLIP J. CRIBB (PC)
Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK

PROF. SID CYWES (SC—DISEAE)
24 Monterey Drive, Constantia 7800, South Africa

DR AMOTS DAFNI (AD)
Laboratory for Pollination Ecology, The Institute of Evolution, University of Haifa, Haifa, Israel

DR SAVERIO D'EMERICO (SD)
Dipartimento di Biologia e Patologia Vegetal, Universitá degli Studi di Bari, via Orabona 4, Bari 70125, Italy

DR RENÉE J. GRAYER (RG)
Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK

DR PETER M. HOLLINGSWORTH (PH)
Royal Botanic Garden, Edinburgh, 20A Inverleith Row, Edinburgh, Scotland EH3 5LR, UK

DR STEVE JOHNSON (SJ)
School of Botany and Zoology, University of Natal, Private Bag X01, Scottsville, Pietermaritzburg 3209, South Africa

DAVID JONES (DJ)
Centre for Plant Biodiversity Research, Australian National Herbarium, CSIRO, PO Box 1600, Canberra, ACT 2601, Australia

DR HUBERT KURZWEIL (HK)
Compton Herbarium, National Botanical Institute, 7735 Claremont, South Africa

DR PETER LINDER (PL)
Bolus Herbarium, University of Cape Town, 7700 Rondebosch, South Africa

DR LUO YI-BO (LY)
Laboratory of Systematic and Evolutionary Botany and Herbarium (PE), Institute of Botany, Chinese Academy of Sciences, Xiangshan, Beijing 100093, China

DR BRIAN MOLLOY (BM)
Botany Division, DSIR, Lincoln, New Zealand

DR M. RUTH M. NEILAND (RN)
Department of Plant and Soil Science, University of Aberdeen, Cruickshank Building, St Machar Drive, Aberdeen, Scotland AB24 3UU, UK

JILLIAN PRESTON (JP)
Royal Botanic Garden, Edinburgh, 20A Inverleith Row, Edinburgh, Scotland EH3 5LR, UK

DR ALEC M. PRIDGEON (AP)
Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK

HELEN RICHARDS (HR)
PO Box 440, Yarra Glen, Victoria 3775, Australia

DR KIM E. STEINER (KS)
Department of Botany, California Academy of Sciences, San Francisco, California 94118–4599, USA

DR NIGEL C. VEITCH (NV)
Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK

DR L. VOGELPOEL (LV)
7, Sunnybrae Road, Rondebosch 7700, South Africa

DR ALEX WIDMER (AW)
Geobotanical Institute, ETH Zürich, Zollikerstr. 107, CH–8008 Zürich, Switzerland

JEFFREY WOOD (JW)
Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK

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I

THE ORIGIN AND BIOGEOGRAPHY OF ORCHIDACEAE

The orchid family, Orchidaceae, has inspired a great deal of speculation concerning the timing and place of their evolution, but since they have no fossil history until the Miocene (Schmid and Schmid 1977; general review in Herendeen and Crane 1995), it has been widely assumed that they are a relatively recently evolved family. In accordance with the putative recency of their origin, it has also been assumed that the orchids represent the pinnacle of monocot evolution, based on the belief that along with the grasses they are among the most highly evolved of monocotyledons. Their highly specialized flowers and habits support this, and with their dust-like seeds, capable of long-distance dispersal, and the high degree of obvious specialization, a recent origin followed by dispersal seems a likely scenario.

First, I would like to review what is currently known about the timing of origin for the angiosperms, with a particular emphasis on monocotyledons and the position of Orchidaceae within them. This will be followed by comments on which traits of the orchids are primitive and some suggestions about how some of this might be evaluated with further study. The age of the angiosperm lineage has been estimated by molecular clocks to be in the Triassic or perhaps earlier (250–350 million years ago (mya); Martin *et al.* 1989; Wolfe *et al.* 1989; Brandl *et al.* 1992). This is a surprisingly early date, given that no undisputed angiosperm fossils are known before the mid-Cretaceous (110–120 mya), but Axelrod (1952) argued for a similar date based on extrapolations from the fossil record. The common ancestor of the angiosperms and any other group of seed plants would almost certainly have been considered a 'gymnosperm' if we had their fossils sitting before us. It is unlikely that we will ever know with certainty which of the extinct gymnosperms were on the direct line that gave rise to the angiosperms because most of the traits that are uniquely angiospermous, such as double fertilization, are unlikely to be fossilized, and those that are likely to be preserved, such as the double integuments enclosing the ovule, may have evolved later.

Origin of the angiosperm lineage and evidence for their early radiation are quite separate topics, and it is clear from the fossil record that angiosperms of many types, both eudicot (*sensu* Chase *et al.* 1993) and eumagnoliid (*sensu* Savolainen *et al.* in press; see below), were abundant and diverse by 110 mya. Brown (1956) and later Cornet (1989) reported a pre-Cretaceous fossil (180 mya), *Sanmiguelia*, which has been compared to some monocots, particularly palms and *Veratrum* (Melanthiaceae: Liliales), and there are also pollen grains from the Jurassic that are similar to those of *Lilium* (Cornet and Habib 1992). These fossils that could be taken as early evidence for the existence of monocotyledons have not been widely accepted (Crane 1989), but it is clear that there should have been angiosperms and perhaps monocotyledons present long before 120 mya. We know little about what pollination strategies might have been operating at such early dates; certainly none of the modern groups of pollinating insects except beetles and flies were present before 120 mya, and so it is difficult to conceptualize what we should be looking for in the fossil record to provide unmistakable evidence for these early angiosperms. The amazing diversity of flowers in extant angiosperms is a clear reminder of the bewildering ability of flowering plants to modify their reproductive structures to fit the available range of pollinating animals, so we might expect that yet older groups of angiosperms were similarly plastic and capable of adapting to the complete range of animals then available, some of which may not now be used as pollinators. Our eyes are trained to recognize forms with which we are familiar, and it is probable that early angiosperms did not look like any extant types; it is unwise to consider that early angiosperms were any less adaptable than extant angiosperms, so the fossil record must be searched without preconceived notions of what is being sought.

Herendeen and Crane (1995) provided the most recent review of the fossil history of monocotyledons, and coupling that information with our much-improved knowledge of monocotyledon phylogeny may provide more robust answers to the question of the timing and early evolution of Orchidaceae than anything previously available. Recent DNA sequence studies based on three genes (two plastid, *rbcL* and *atpB*, and one nuclear, 18S ribosomal DNA; Chase *et al.* 2000) have indicated with high levels of internal support that the basal-most groups are Acoraceae and the families of Alismatales (*sensu* the Angiosperm Phylogeny Group 1998), Araceae, Alismataceae, Butomaceae, Tofieldiaceae, Potamogetonaceae, Hydrocharitaceae, etc. These are followed by the lilioid orders, Asparagales, Dioscoreales, Liliales, and Pandanales, as well as the large commelinoid group composed of Arecales, Commelinales, Poales, and Zingiberales (Fig. I.1). From this we can infer relative dates of appearance for these various lineages; groups that branch later serve as the minimum date for those that precede them in the branching scheme.

The monocotyledon family for which the earliest uncontested fossils are known is Arecaceae, roughly 90 mya (Christopher 1981),

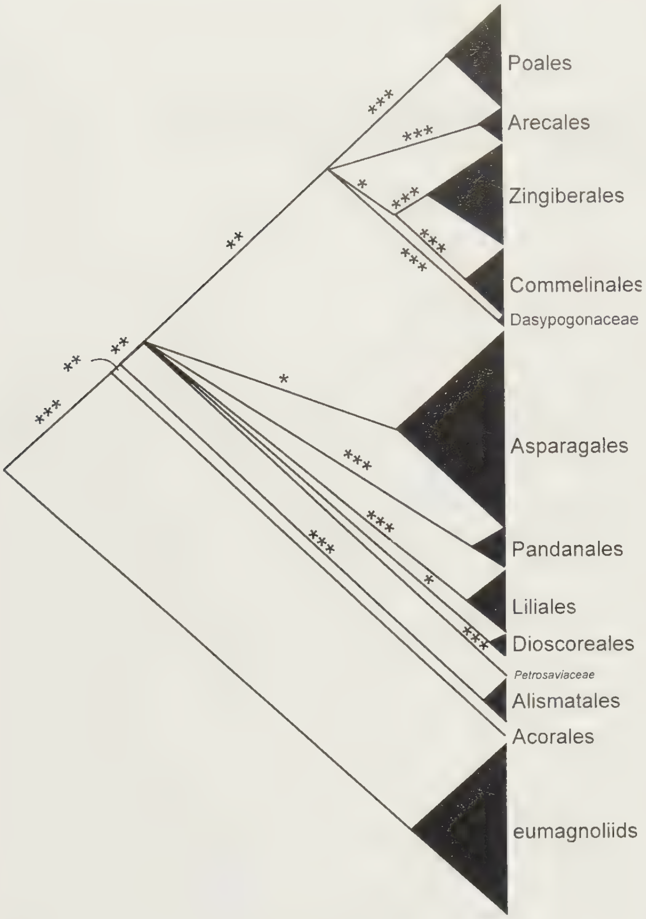

Fig. I.1. The bootstrap consensus tree from Chase *et al.* (2000) for the monocots plus outgroups (the eumagnoliids) based on three genes analysed together: plastid *atpB* and *rbcL* and 18S nuclear ribosomal DNA. Orchidaceae are positioned near the base of Asparagales. *** = strong bootstrap support; ** = moderate support; * = weak support.

and thus all groups that branch before the palms are at least this old; this would include Acorales, Alismatales, Asparagales, Dioscoreales, Liliales, and Pandanales. If one can assume that palms are slightly older than their first appearance in the fossil record and that all of these other orders are therefore even older, then a reasonable estimate for the age of the lilioid orders is 100–110 mya with the ages of Acorales and Alismatales being 140–120 mya. This accords well with the appearance in the fossil record and subsequent radiation of the eumagnoliids about 120–100 mya (*sensu* Savolainen *et al.*, in press; Soltis *et al.*, submitted; e.g. Chloranthales, Laurales, Magnoliales, Piperales, and Winterales), which are the collective sister group for monocotyledons.

All recent studies of DNA sequences have placed Orchidaceae in a group of families to which the rest of Asparagales are sister (Chase *et al.* 1995; Rudall *et al.* 1997; Chase *et al.* 2000): Asteliaceae, Blandfordiaceae, Boryaceae, Hypoxidaceae, and Lanariaceae. The next most closely related families are Doryanthaceae, Iridaceae, Ixioliriaceae, and Tecophilaeaceae. If the orchids, which are nearly at the base of Asparagales, are similar in age to Asparagales, then they also evolved approximately 110 mya, at which time all of the major continents were close enough to have been occupied by orchids without the need for long intercontinental dispersal. Most orchids are not able to disperse regularly over great distances (Dressler 1981), but, as Dressler pointed out (1981), in geological time even a small possibility of intercontinental dispersal is greatly amplified. However, since Orchidaceae evolved at a time when the continents were all reasonably close to each other, dispersal was not the problem that it now is. The problem of orchid origins, that is, on which continental mass they evolved, is a speculation without hope of evidence. The first orchid clearly had to appear only in one location, but on which of the early continents this occurred will never be answered with confidence. It is possible only to say that the orchids evolved early enough to have been widespread long before the continents moved away from each other. Some have pointed to the Asian tropics in which the apostasioids now occur as the home of the original orchids, but at the time the family evolved this area had not yet emerged from the sea.

Among the 'lower' Asparagales, only three families are widely distributed outside of the southern hemisphere: Hypoxidaceae, Iridaceae, and Orchidaceae. This could be taken as an indication that all of these families evolved in and later dispersed from Gondwanaland, leaving behind most of their close and less species-rich relatives, but instead the pattern is largely relictual for all of these families with only the evolutionarily most successful families retaining something like their original distribution. Representatives of the other families now confined to the southern hemisphere are relicts of groups that were at one time perhaps as widely dispersed as Hypoxidaceae, Iridaceae, and Orchidaceae are now. This scenario best explains why we see *Ixiolirion* (Ixioliriaceae) in western and central Asia and *Odontostomum (*Tecophilaeaceae) in western North America (California); these genera are the only remaining evidence of these families' previous existence outside the southern hemisphere, and their occurrence in these areas is just as relictual as those now found only in the southern hemisphere. The north temperate zone contains many fewer groups with relict distributions because of the considerable effects of glaciation that never occurred as extensively in the southern hemisphere.

Some recent monocot classifications have treated the orchids as comprising several families, for example Apostasioideae, Cypripedioideae, and Orchidaceae *s. str.* (F. N. Rasmussen in Dahlgren *et al.* 1985), based on the synapomorphy of a single anther for Orchidaceae *s. str.*, which thus excludes the apostasioids and cypripedioids. This produces a more homogenous set of families, but confuses the issue of whether the excluded groups are still each others' closest relatives as well as ignoring whether or not the excluded groups exhibit their specializations for the same reasons as the monandrous orchids—common ancestry. DNA sequence data clearly place these three clades together in a well-supported monophyletic group (Chase *et al.* 1994; Cameron *et al.* 1999; Chase *et al.* 2000), and there seems little to be gained by excluding these two small and somewhat deviating groups from Orchidaceae. They exhibit the other synapomorphies typical of the family, and against the background of their closest relatives in Asparagales they make an easily delimited larger taxonomic group. Exclusion on the grounds of greater homogeneity leads only to a more complicated taxonomy and a loss of phylogenetic information. The apostasioids and cypripedioids are clearly orchids in a general sense and are best treated as members of Orchidaceae.

Several authors (Dressler 1981, 1993; Garay 1960, 1972) have speculated on which characteristics of orchids are primitive, and Dressler (1993) built a composite of traits to produce a hypothesis for the appearance of the early orchids, which I take to mean the last common ancestor of the lineages that came to be the orchids and the other families of Asparagales. These included being rhizomatous and sympodial with erect and perhaps branching and twining shoots on which flowers were borne terminally, perhaps in bracteate racemes; leaves were spirally arranged and plicate. Flowers had inferior ovaries divided into three locules, and they almost certainly had six stamens that shed their powdery pollen inwardly; the fruits were fleshy, and the small seeds had a hard seed coat. At the time Dressler wrote this description (which was published in 1993), the exact position among the monocots for the orchids was only beginning to be elucidated by studies of DNA sequences (Chase *et al.* 1993; Duvall *et al.* 1993), and so it is worthwhile revisiting this description in the light of the other families positioned among the lower Asparagales (*sensu* Chase *et al.* 1995). The branching/twining habit described by Dressler is unknown in these families (although it is present in some members of Hemerocallidaceae and Tecophilaeaceae), but it is not for me to suggest that this hypothesis is wrong. The outgroup approach is best applied to groups in which little extinction has occurred, and Asparagales as a whole have a highly relictual distribution (meaning that extinction elsewhere has been extensive), thus making such optimizations unlikely to be informative (too many extinctions ruin optimizations). They now occur in what may be an atypical habitat relative to that in which they originally evolved; nearly all of the close relatives of the orchids occur in areas that have recently (geologically speaking) experienced aridification: Australia for Asteliaceae, Blandfordiaceae, Boryaceae, and Doryanthaceae; South Africa for Lanariaceae and many genera of Hypoxidaceae and Tecophilaeaceae; southern coastal South America for other Tecophilaeaceae; and central and middle Asia for Ixioliriaceae.

If these families shared a common ancestor approximately 90–100 mya, then they would have most likely been tropical plants adapted to uniformly warmer and moister conditions rather than the xerophytically modified taxa that we observe today. The only mainly tropical genera in these closest families are *Hypoxis* and *Curculigo* (both Hypoxidaceae), *Aristea*, and *Geosiris* (both Iridaceae, the latter an achlorophyllous mycotroph), and *Cyanastrum*, *Kabuyea*, *and Walleria* (all Tecophilaeaceae). If one uses these taxa to construct a hypothetical ancestor, then Dressler's ideas compare quite favourably.

I would suggest the following modified scenario: the common ancestor of these plants was certainly sympodial and rhizomatous with a short, erect, and probably unbranched and non-vining stem (branching is unknown in these families except for some woody genera of Iridaceae, such as *Nivenia*, *Witsenia*, and *Klattia*, and twining is only present in *Walleria* of Tecophilaeaceae); velamen on the roots may have been present because a similar structure has been reported in other members of Asparagales; flowers were more likely produced from the axil of each leaf on a separate stem, which is typical in all these taxa; the leaves were likely to have been plicate or at least broad (as in *Cucurligo* of Hypoxidaceae); the flowers would have had an inferior ovary divided into three locules and six stamens that opened outwardly, releasing powdery pollen; and the fruits would have been dry capsules (not fleshy) with small seeds with a hard seed coat. I presume that this plant grew in the understorey of a wet tropical forest, and it would have been evergreen and perhaps mycorrhizal, perhaps similar in habit to *Calanthe*, *Nervilia*, and some of the stemless species of *Cypripedium*. The transition between stemless and stemmed is an easy one and is merely due to an elongation of the sympodium and/or the addition of several more nodes to the stem; length of the stem also affects the position of the inflorescence so that the shift from a lateral to a terminal position is simply a matter of stem elongation. The inflorescence in all sympodial plants is probably lateral (in that it occurs from the lateral bud of the last leaf or bract). When it occurs from the base of the last leaf at the end of a long stem it is usually described as 'terminal', whereas when it is from the base of a stemless leaf it is 'lateral'. In any event, it is easy to see that the difference between Dressler's concept (1993) and mine here is relatively trivial and a matter of where on the continuum of stemmed to stemlessness the favoured habit is placed; if *Nervilia* and *Calanthe* are one extreme and *Tropidia* and *Xerorchis* the other, then such taxa as *Palmorchis* and *Monophyllorchis* fall in the middle. There are no asparagoid lilies with stamens opening toward the inside, nor do asparagoid lily families nearest to orchids have fleshy fruits (except in genera such as *Astelia* of Asteliaceae and *Empodium* of Hypoxidaceae), so it unlikely that the last common ancestor of the orchids and other asparagoid lilies had either of these traits.

Although Orchidaceae are highly evolved (see below), they are reasonably early-emerging monocots and do not in a phylogenetic sense represent one of the more terminal (recently evolved) lineages. They are typical members of the 'lower' Asparagales (Chase *et al.* 1995; Rudall *et al.* 1997) in having inferior ovaries, simultaneous microsporogensis and septal nectaries (as opposed to Liliales, which all lack such nectaries; Rudall *et al.* 2000). The issue of 'evolutionary advancement' as a measure of phylogenetic position is often confused in many people's minds, and this is a perfect example of a situation in which it is highly misleading. Orchid flowers are in no respect primitive within the context of Asparagales in particular or monocots in general; they are highly and consistently organized, synorganized, or canalized (see below), such that the parts of their flowers have a definite orientation relative to each other, which makes possible the marvellously bizarre and complex relationships many orchids exhibit with their pollinators. Other more 'advanced' members of Asparagales, such as Asphodelaceae and Anthericaceae *s. str.* (Chase *et al.* 1996) have more typically monocot flowers. We are so accustomed to thinking of the more highly specialized organisms as the 'most advanced' and recently evolved that we miss the fact that old lineages can also become highly specialized, leaving more recently evolved groups to exhibit the ancestral traits of their larger lineage (in this case Asparagales). The families of lower Asparagales all are highly specialized in different ways, and in this respect Orchidaceae, Iridaceae, Tecophilaeaceae, and Hypoxidaceae have all deviated substantially from the generalized format found in many monocots, but unique specializations tell us nothing about phylogenetic position or recency of origin. Evolution does not often produce progressively more advanced lineages as it proceeds; specializations occur in both the more highly derived recent groups as well as some of the earliest branching taxa. In the case of the orchids, emphasis on their highly modified flowers obscured the fact that orchids have close relatives and do not occupy the pinnacle of monocot evolution that some taxonomists (Stebbins 1974; Cronquist 1981) envisioned. This is not an argument against viewing them as highly evolved (because they are) but rather against over-interpretation in the absence of a clear idea of monocot evolution. Orchids do not occupy the apex of monocot evolution but still represent one of the most highly evolved sets of life history strategies on Earth. The problem is one of confusing specialization with phylogenetic recency and phylogenetic derivativeness; the latter must be addressed on a phylogenetic tree, not by emphasis on unique traits exhibited by the plants under consideration.

Orchidaceae evolved early enough that we should expect some genera to display distributions representative of the classic tropical disjunctions from that period: South America, Africa, and Asia. This is met in genera such as *Calanthe*, *Corymborkis*, *Goodyera*, *Habenaria*, *Liparis*, *Malaxis*, *Tropidia*, and *Vanilla* and groups of genera such as *Monophyllorchis/Diceratostele* (South America/western Africa), *Xerorchis/Nervilia* (South America/Africa/Asia), and *Selenipedium/Phragmipedium/Paphiopedilum* (South America/Africa/Asia). Genera or groups of closely related genera with this distribution occur in each subfamily (Chase *et al.* 1994; Cameron *et al.* 1998), except in Apostasioideae. *Aspostasia* and *Neuwiedia* are found only in the Asian tropics, but this distribution is indicative of their extinction elsewhere in tropical zones given that other similarly basal genera in the family occur in all three tropical zones (e.g. *Corymborkis*, *Tropidia*, *and Vanilla*). Additional genera that are widespread include *Bulbophyllum*, *Cymbidium* (and closely related African genera), *Disperis*, *Phaius*, *Polystachya*, *Satryium*, and *Zeuxine*. Until we know more about their specific phylogenetic relationships it would be premature to conclude that these are not the result of more recent long-distance dispersals. Tribes and subtribes that evolved after the continents were widely separated are presently confined to one region. Examples of this include Catasetinae, Dendrobiinae, Epidendreae, Eriinae, Maxillariinae, Oncidiinae, Podochilinae, Stanhopeinae, and Zygopetalinae.

Modern groups of insect pollinators, such as Hymenoptera, do not appear in the fossil record until about 100–110 mya (Wilson *et al.* 1967; Zeuner and Manning 1976), and it seems likely that plant families such as Orchidaceae, in which evolutionary diversification must have depended on pollinators capable of complex behaviour, could not have existed much before these dates. The flowers of Orchidaceae are highly organized/canalized (synorganized), and this makes utilization of other groups of less specialized pollinators such as dipterans possible, but it is not certain that orchids could have been ancestrally pollinated by such insects. It is more likely that the specializations that evolved in parallel with the appearance of hymenopterans then made possible adaptations to dipterans and also yet more highly specialized pollinators, such as birds, lepidopterans, euglossine and various oil-collecting bees, and the vast array of deceit systems that operate throughout the family. The similar highly synorganized families of eudicots that depend on the more advanced insects as pollinators appear in the fossil record at about the same time (90–100 mya; Crepet and Nixon 1998); thus it is reasonable that the orchids also radiated at approximately this time. The other highly synorganized family of Asparagales—Iridaceae—probably diversified at this same time, and that deviation from the standard monocot flower format (two whorls each of unmodified tepals and stamens) may be responsible for the evolutionary success of such monocot families (including families in Commelinales and Zingiberales) as it has been for many eudicot families.

A great deal has been written about co-evolution and how it enables 'leap-frog' radiations in pollinators and flowers, but orchids have apparently either given up such a role or perhaps only rarely played it. Orchid flowers in general operate by deceit. It may only have been possible for orchids to have diversified extensively once the more tightly co-evolutionary relationships among pollinators and flowers evolved in other groups, making it possible for orchids to co-opt these strategies and mimic other flower types, thus being pollinated without offering a reward to the pollinator. Such highly evolved life history traits, rather than being evolved recently, may instead only develop if a long and stable period is available. This may explain why so many more highly specialized groups occur in the tropics and the southern hemisphere than in the northern hemisphere, where recent glaciation has had a profound effect and reduced the number of lineages present and the diversity within them.

In summary, for the first time in the history of orchid study, we can proceed with a range of studies based on a much clearer perspective about monocot relationships and the position of orchids within them. The orchids are members of Asparagales, along with other highly specialized families such as Hypoxidaceae and Iridaceae. The order almost certainly evolved before the end of the Cretaceous, and the orchids as one of the first-diverging families within the order must have an origin and diversification shortly thereafter, probably contemporary with the diversification of the higher insect groups that are suited to be able to operate the complex, synorganized flowers of Orchidaceae. Although orchids are capable of long-distance dispersal, which has played a role in some of the more recently evolved groups, the geographic patterns that orchids exhibit are largely those associated with plate tectonics. In terms of their evolutionary history, Orchidaceae are an old, uniquely specialized group of monocotyledons that has been successful as a result of synorganization of the generalized flower format typical of most insect-pollinated monocots. They have evolved such specializations in parallel with many groups of highly and similarly advanced dicots. Given that orchids are masters of deceit, they may have been able to diversify extensively only once the more tightly co-evolutionary relationships between pollinators and flowers evolved in other families, making it possible for orchids to become parasites on their pollinators in the same way that they begin their lives as parasites of fungi. Although the evidence for the position of Orchidaceae stems largely from analyses of DNA sequences, it is highly congruent with biogeographic and evolutionary patterns that are becoming apparent from other lines of evidence as well. Integrating evolutionary studies of orchids into this developing scenario is the exciting future awaiting all scientists interested in orchid biology.

MARK W. CHASE

II

ORCHIDOIDEAE (Part 1)

Orchidoideae. Lindl., *Coll. Bot.*, *App.* (1826). Type: *Orchis* L.

Subfamily Ophrydoideae Burnett, *Outlines Bot.*, 461 (1835), as Subtypus Ophrydeae; Garay in *Bot. Mus. Leafl. Harvard Univ.*, **19** (3), 87 (1960). Type: *Ophrys* L.

Subfamily Spiranthoideae Dressler in *Selbyana*, **5**, 204 (1979) and *Orch.: Nat. Hist. Class.*, 166–176 (1981). Type: *Spiranthes* L.C. Rich.

Note: A large proportion of taxa traditionally included in Neottioideae (but excluding the type *Neottia*) are now considered members of Orchidoideae.

Description

Terrestrial or rarely epiphytic *plants* with root tubers, stem tubers or fleshy, short to long rhizomes, sometimes holomycotrophic with leaves reduced to colourless sheaths. *Tubers*, if present, ovoid, spherical, ellipsoidal or cylindric-fusiform, solitary or in clusters, hairy or glabrous. *Rhizome*, if present, fleshy, elongate. *Leaves* spirally arranged, one to many, basal or arranged along the stem, deciduous or rarely persistent for more than one year, often sheathing at the base, the lowermost reduced to sheaths, the uppermost often bract-like, usually green, rarely spotted or veined with silver, red or gold, sometimes purple-spotted or shaded beneath. *Inflorescence* terminal, erect or arching, one- to many-flowered, rarely secund; peduncle usually terete, glabrous, hairy or glandular; bracts linear, lanceolate, ovate or elliptic, sometimes cucullate, usually glabrous and green. *Flowers* small to large, usually resupinate, flat to tubular, often showy, green, white, yellow, pink, purple or red; pedicel usually short, often obscure. *Dorsal sepal* free or often adnate to the petals to form a hood over the column. *Lateral sepals* usually free, sometimes connate and oblique at base to form a spur-like mentum, rarely connate to the base of the column, lip, stigma lobes or rostellum. *Petals* entire or two-lobed, often adnate to dorsal sepal. *Labellum* usually lowermost in flower, usually deflexed, entire, three- or five-lobed, or bipartite, occasionally callose or with two basal

Fig. II.1. Distribution map of Orchidoideae.

glands, often spurred or saccate at the base; spur saccate, scrotiform, fusiform, clavate or cylindrical, rarely fused to the ovary. *Column* basifixed, rarely adnate to the other floral segments at the base, erect or decumbent; anther bilocular, longer than or as long as the rostellum, locules either adnate, divergent or separated on a more or less broad connective; pollinia two or four, sectile, attached by short to elongate caudicles to one or two viscidia; staminodes two, usually present, sessile or stalked, usually shorter than the column, rarely filiform and as long as or longer than the column; stigma entire or two-lobed, sessile or stalked, concave to convex; rostellum usually two- or three-lobed, shorter than or as long as the anther, sometimes obscure, when three-lobed the mid-lobe erect or porrect, lying between or in front of the anther loculi, the side lobes short to long, porrect, rarely incurved or upcurved. *Ovary* distinct, glabrous or less frequently hairy/glandular. **(PC)**

Distribution (Fig. II.1)

A subfamily comprising seven tribes, with about 3630 species, well represented in northern temperate and tropical areas of both the Old and New Worlds. The subfamily is particularly well represented in Europe, tropical and South Africa, Madagascar, temperate Australia, North America, and temperate South America. **(PC)**

Phylogenetics

The monandrous orchids have a long history of recognition in orchid classification, but the subdivisions within them have varied greatly. One of the consistent features of nearly all systems of orchid classification has been the recognition of Orchidoideae, which must contain the type genus of the family, *Orchis*. Circumscription of Orchidoideae has been inconsistent, varying from a more broadly delimited version including all monandrous orchids (Dressler and Dodson 1960) to a taxon comprising only the predominantly terrestrial orchids with root tubers including most of the familiar European orchids as well as the Australian Diurideae and principally African Diseae (e.g. Dressler 1981, 1983, 1993). Nearly all systems (for exceptions see Lindley (1830–40) and Mansfeld (1937) have separated them from the spiranthoid orchids, most of which lack root tubers and have been variously consigned to Neottioideae (Rasmussen 1985) or Spiranthoideae (Burns-Balogh and Funk 1986*a*, *b*; Dressler 1981, 1983, 1993). Several tribes have been shifted back and forth between the various concepts of Orchidoideae and Spiranthoideae, most notably Diurideae.

The concept of subfamily Orchidoideae used here is much enlarged over that of Dressler (1993). Dressler included within the subfamily those orchids that have 'root-stem' tubers, soft leaves, stomata with no subsidiary cells, an acute column apex and relatively large chromosomes. Senghas (1973–1974) recognized three tribes within Orchidoideae: Orchideae, Diseae, and Satyrieae, essentially those monandrous orchids with basitonic anthers. Dressler (1993), however, included Satyrieae as a subtribe of Diseae and added Diurideae to Orchidoideae.

Spiranthoideae (Burns-Balogh and Funk 1986; Dressler 1993) have often been treated as a tribe, Cranichideae, in Neottioideae (Brieger 1974; Garay 1972; Rasmussen 1985). These in contrast to Orchidoideae lack tubers and have definite hemimesoperigenous subsidiary cells (Rasmussen 1981). Dressler (1993) additionally used terminal (acrotonic) anthers and *Goodyera*- and *Spiranthes*-type seeds to delimit Spiranthoideae (in which he included Diceratosteleae and Tropidieae), but both of these characters are found as well in Diurideae (seed descriptions in Molvray and Kores 1995). Thus, as Kores *et al.* (1997) observed, Spiranthoideae are monandrous orchids lacking the distinguishing features of Orchidoideae and Epidendroideae, and such a 'definition' was certain to obscure their real relationships.

Kores *et al.* (1997) published a phylogenetic analysis of DNA sequence data from the plastid *rbcL* gene of 53 orchid species. The results indicated that Cranichideae (Spiranthoideae *sensu* Dressler 1993) are nested within an orchidoid clade together with Chloraeinae, Pachyplectroninae, and Pterostylidinae, which collectively are sister to Diurideae (Orchidoideae *sensu* Dressler 1993). Diceratosteleae and Tropidieae, also assigned by Dressler (1993) to Spiranthoideae, are members of Epidendroideae, falling near taxa such as *Monophyllorchis*, *Nervilia*, *Palmorchis*, and Neottieae (*Cephalanthera*, *Epipactis*, and *Listera*). In a yet larger analysis of Orchidaceae as a whole, also using *rbcL* (Cameron *et al.* 1999), the same pattern was obtained. Other as yet unpublished DNA sequence data from the plastid gene *matK* and the largely non-coding plastid *trnL-F* region corroborate this result (Kores *et al.*, unpublished). These results indicated that seed characters are more reliable than underground structures and column morphology for assessing relationships. Freudenstein and Rasmussen (1999) have conducted the most extensive cladistic analysis of morphological characters of Orchidaceae published so far (Burns-Balogh and Funk (1986) did not use an algorithm or search procedure). Although their results are not in strict agreement with the DNA analyses, their trees also embed Cranichideae within Orchidoideae, more or less as the sister group of Diurideae (plus Orchideae/Diseae). Furthermore, Freudenstein (1991) and Freudenstein and Rasmussen (1999) found that the spiranthoids (Cranichideae) share a form of endothecial thickening and patterns of pollinia development with Orchideae, Diseae, and Diurideae, and these traits can thus be viewed as synapomorphies for an expanded concept of Orchidoideae. In Freudenstein and Rasmussen (1999), other synapomorphies for Orchidoideae/Spiranthoideae include absence of schlerenchyma in their non-plicate (fleshy) leaves, spiral phyllotaxy, polygonal epidermal cells, and intercellular spaces in seed testa. The first two of these characters resulted in *Listera* being positioned as the sister genus of Orchidoideae/Spiranthoideae with equal weighting (although with implied weighting the sister group is a grade of five genera including *Listera*). These are clearly parallelisms because *Listera* is a member of Epidendroideae, leaving these as synapomorphies for Orchidoideae/Spiranthoideae.

In agreement with these studies, we consider Cranichideae to be members of Orchidoideae, and Diceratosteleae and Tropidieae to

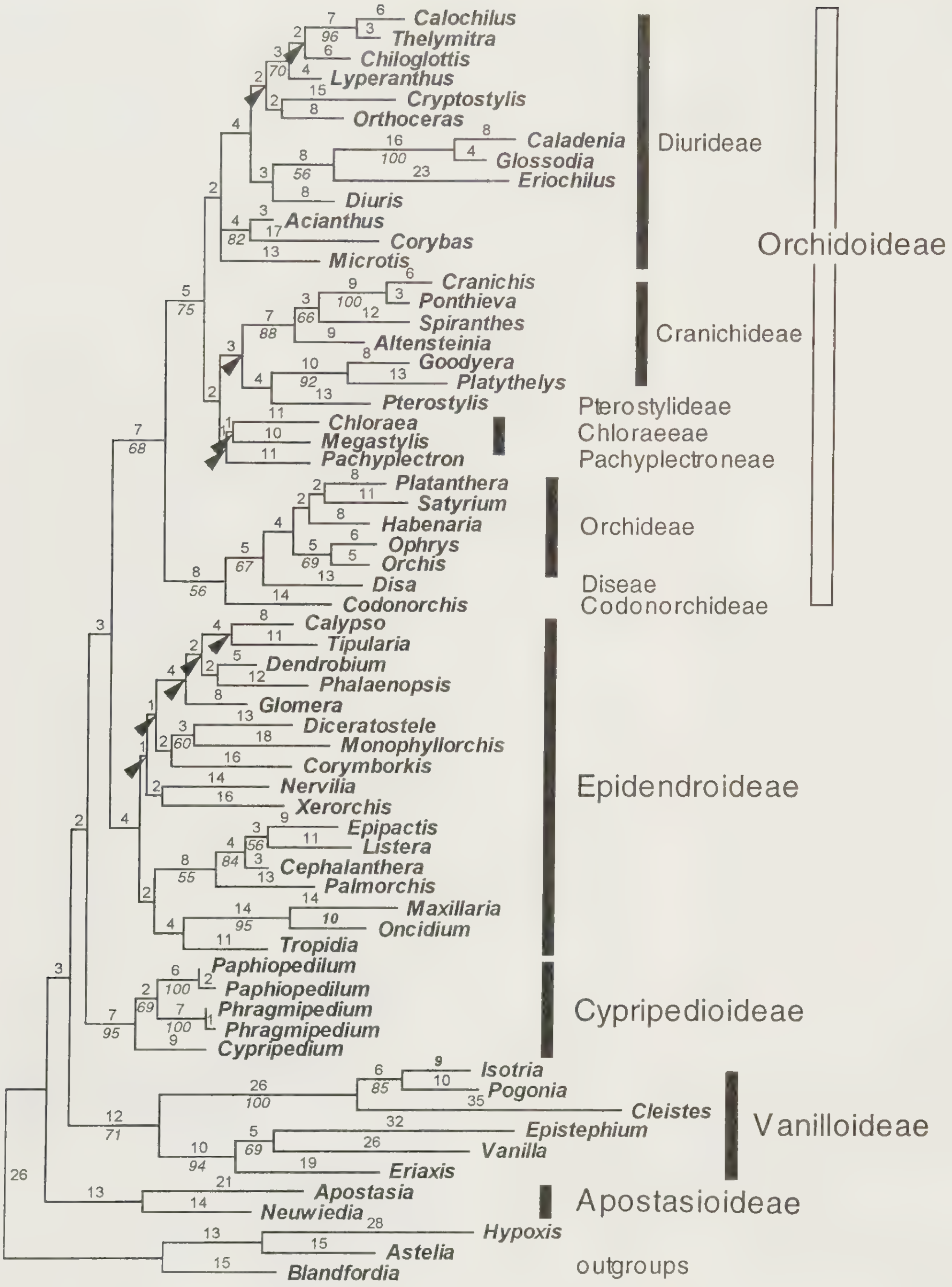

Fig. II.2. One of the shortest *rbcL* trees found using PAUP* 4.0 in a standard heuristic search (equal weights, 1000 random replicates, with SPR swapping, and 250 bootstrap replicates). This tree is one of 448 equally most parsimonious trees from a single island with a consistency index of 0.49 (including autapomorphies) and a retention index of 0.57. Numbers above the branches are the estimated substitutions (ACCTRAN optimization); numbers below in italics are bootstrap percentages (branches without a bootstrap percentage received <50%). Arrows indicate groups not present in the strict consensus tree of all 448 trees. Subfamilies and tribes indicated are those being followed in *Genera Orchidacearum*. Voucher information and accession numbers are as cited in Kores *et al.* (1997) and Cameron *et al.* (1999).

be members of Epidendroideae. Although subfamilial relationships appear now to be clearly resolved based on corroborative studies of the DNA and morphological data, relationships of the tribes and subtribes within Orchidoideae are still in an active state of investigation as this text goes to press.

Orchideae are commonly defined by the presence of a spur on the frequently three-lobed lip, and Diseae by their anther that is usually reflexed to a horizontal or pendent position (Dressler 1981, 1993; Linder 1986*a*). In Orchideae the rostellum is frequently small, whereas it is usually large in Diseae (Linder 1986*a*). However, a number of exceptions in both tribes have repeatedly been pointed out (Schlechter 1901; Linder 1986*a*; Kurzweil and Weber 1992), leaving doubt about the taxonomic significance of the anther orientation. The basitonic anther, which is firmly attached to the rest of the column was the first character used to separate Orchideae from other orchids with sectile pollinia. Auricles on the sides of the column, composed of basal bulges (which are most likely staminodes) and appendages of the fertile anther, were recognized and described by Kurzweil (1987, 1988, 1989, 1990*a*, *b*, 1991). Freudenstein and Rasmussen (1999) were not confident about assigning the homologies of these structures across Orchidaceae and consequently did not use the auricles in their phylogenetic analysis. Finally, the deeply three-lobed rostellum with two viscidia is common in the two tribes. All of these characters have exceptions in Orchideae and Diseae, but these are probably specialized developments and will be discussed under the respective genera.

In addition to the studies of Kores *et al.* (1997), Freudenstein and Rasmussen (1999), and Cameron *et al.* (1999), several additional papers relevant to tribal delimitation of Orchideae/Diseae have been published. Pridgeon *et al.* (1997) investigated relationships in Orchideae, and Douzery *et al.* (1999) studied Diseae in great detail. Both of these indicated that there are still problems with the classification adopted in this volume. Orchideae appear to be monophyletic, but their component subtribes *sensu* Dressler (1993) are not; for example Diseae are paraphyletic to Orchideae. Douzery *et al.* (1999) analysed only DNA sequences of the internal non-transcribed spacer region (ITS) of nuclear ribosomal DNA to assess relationships of Diseae, but their results have been mirrored by those from analyses of plastid *matK* and *trnL-F* sequences (Kores *et al.*, unpublished). Diseae form a grade in all cases. Freudenstein and Rasmussen (1999) also failed to obtain a monophyletic Diseae in their analyses. It thus appears that Diseae will need to be dismembered, with Satyriinae perhaps fitting better in Orchidinae.

Pterostylidinae, Pachyplectroninae, and Chloraeinae need to be transferred from Diurideae, and because they are successive sister groups to Cranichideae in combined analyses of *rbcL*, *matK*, and *trnL-F* (Kores *et al.*, unpublished), they perhaps need to be elevated to tribal status. Likewise *Codonorchis* falls outside of Chloraeinae as sister to Diseae/Orchideae, so it too must be elevated to tribal status (Cribb and Kores, in press). *Codonorchis* is unusual in Chloraeinae in having tubers, and M. Clements (personal communication) reported that it also has an embryo form that is different from others in Orchidoideae.

To summarize the current taxonomic status of tribes in Orchidoideae, we have supplemented the published *rbcL* matrix of Kores *et al.* (1997) with additional sequences from Cameron *et al.* (1999) and a new *rbcL* sequence of *Codonorchis* (van den Berg and Chase, unpublished) and run a phylogenetic analysis using standard heuristic methods. These results (Fig. II.2) are consistent with previous analyses, and the new sequence for *Codonorchis* falls as sister to Diseae/Orchideae. The taxonomic scheme indicated in the side bars is the one followed here; we acknowledge that several problems exist with the monophyly of some of these tribes (e.g. Diseae), but it is premature to proceed with re-circumscription until more studies are completed. **(MWC, HK, PL, PC)**

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Artificial key to the tribes of Orchidoideae (PC)

1. • Plants with root tubers or stem tubers 2
   • Plants lacking root tubers or stem tubers, usually rhizomatous or with fasciculate fleshy roots 6

2. • Viscidium single; pollinia sectile or not, usually lacking caudicles; column usually constricted at base of anther 3
   • Viscidia usually 2; pollinia sectile, usually with more or less prominent caudicles; column not constricted at anther base 4

3 • Column slender, elongate, arcuate, with retrorse axe-shaped apical wings on either side of anther; labellum motile, sensitive with a basal appendage .... **Tribe Pterostylideae**
  • Column and labellum lacking the above .... **Tribe Diurideae**

4 • Column short, lacking a foot; anther bilocular, the loculi opening by longitudinal slits, not operculate 5
  • Column slender, elongate, with an elongate foot at the base; anther operculate .... **Tribe Codonorchideae**

5 • Anther erect; labellum with a single basal spur or lacking a spur .... **Tribe Orchideae**
  • Anther bent back from the column or recumbent, with the base uppermost; spurs various, double if formed by the labellum .... **Tribe Diseae**

6 • Rhizome absent; roots fasciculate; viscidium absent .... **Tribe Chloraeeae**
  • Rhizome usually present; roots clustered or scattered along rhizome; viscidium present .... **Tribe Cranichideae**

A. TRIBE DISEAE

Diseae (Lindl. ex Benth.) Dressler, *Selbyana*, **5**, 204 (1979). Type: *Disa* Bergius.
Subtribe Disidae Lindl., *Veg. Kingd.* ed. 2, 182 (1846), *sine descr.*
Subtribe Disinae Lindl. ex. Benth., *J. Linn. Soc.* (*Bot.*), **18**, 288 (1881) (as Diseae).

Description

Terrestrial *herbs*, almost always glabrous in all above-ground parts, with root tubers, rarely in addition to this with stolons. *Tubers* annual, globular to elongate, 3–25 mm in diameter, unlobed but apically sometimes bifid. *Stems* normally upright, ranging from slender and wiry to stout. *Leaves* radical, basal or cauline, undivided, mostly narrowly lanceolate or linear, sometimes broadly ovate and occasionally adpressed to the ground. *Inflorescence* a terminal, unbranched, elongate raceme or head-like cluster, rarely single-flowered. *Flowers* small to large, resupinate or not, throughout with striking colours or green sepals. *Dorsal sepal* unlobed, often galeate and spurred, sometimes adnate to the petals to form a hood, frequently apiculate. *Lateral sepals* unlobed, spreading or reflexed, rarely saccate, frequently apiculate. *Petals* spreading, included in the dorsal sepal galea, exserted from it or adnate to it; with various shapes ranging from lorate to falcate, but usually undivided although sometimes apically bifid, often with a basal anticous lobe, frequently fused at the base with the column; very rarely stalked, saccate and marginally fringed. *Labellum* either simple and without spur or galeate with two separate spurs, normally as long as or longer than the column, rarely minute; in Coryciinae basally fused with the column and with a massive basal appendage, sometimes in addition with a laminal callus. *Column* with or without prominent undifferentiated stalk; anther with two normally parallel thecae, thecae either adjacent or situated on the corners of a long horseshoe-shaped connective, thecae horizontally reflexed or pendent, rarely erect or suberect, globose to elongate, anther rarely with a signifi-

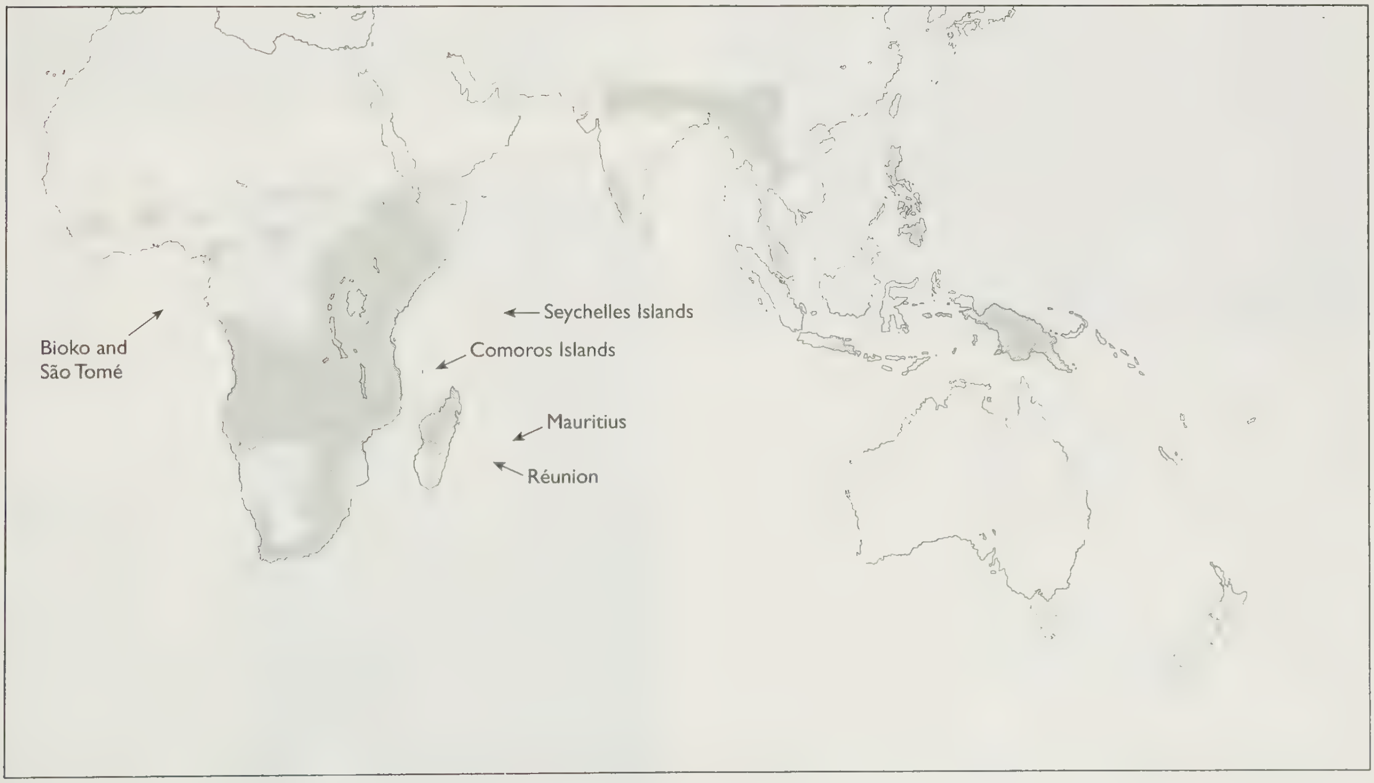


Fig. A.1. Distribution map of Diseae.

cant terminal connective process; lateral appendages mostly prominent and sculptured; pollinia two, sectile, with globose to disk-like viscidia; stigma pad-like and often tripulvinate or flap-like, usually derived from all three carpels, rarely only from the median one; rostellum tall, either three-lobed with large or small central lobe, two-lobed or unlobed; usually with two separate viscidia, very rarely with only one viscidium.

Distribution (Fig. A.1)

The group is largely African and Madagascan in distribution, although both *Disperis* and *Satyrium* range into Asia. Diseae comprise about 400 species in 11 genera. Five subtribes, Satyriinae, Disinae, Brownleeinae, Huttonaeinae, and Coryciinae are currently recognized (Linder and Kurzweil 1994). **(HK, PL)**

Anatomy

The vegetative anatomy of Diseae was surveyed in detail by Kurzweil *et al.* (1995). From all 11 genera, 123 species have been studied. Previously, leaf anatomy of a large number of Disinae and Coryciinae was studied by Chesselet (1989). Investigations of the vegetative anatomy of the Asian *Satyrium nepalense* D. Don are also available (Rao and Sood 1979; Kumar and Manilal 1986). In most characters the vegetative anatomy was found to be fairly uniform in the tribe. However, the degree of dissection of the siphonostele of the tubers ('monostelic' versus 'polystelic') as well as the presence of a sclerenchyma cap on the leaf vascular bundles differ extensively among the species studied. Both characters were regarded as taxonomically significant. The following discussion is a summary of the papers of Kurzweil *et al.* (1995) and Chesselet (1989).

Leaf

Hairs absent except in *Disa glandulosa* Burch. ex Lindl., *D. vaginata* Harv. ex Lindl., and a few *Disperis* species; margins are ciliate in *Ceratandra atrata* (L.) T. Dur. & Schinz and *C. globosa* Lindl. Cuticle usually thin (3–5 μm) but slightly thicker in *Disa* sections *Stenocarpa* and *Herschelianthe* (up to 10 μm), ornamentation variable within the same species and within the same leaf, ranging from striate to reticulate or punctate. Epidermis: cells normally isodiametric, with the cells of the lower leaf epidermis often larger than those of the upper. A massive upper epidermis, 4–15 times as thick as the lower, occurs in *Satyrium*. Stomata anomocytic, abaxial or more rarely on both surfaces, normally 45–100 μm long and 40–100 μm wide, with species of *Satyrium* having particularly large stomata. Mesophyll mostly homogeneous or weakly heterogeneous. A distinctly heterogeneous mesophyll occurs mainly in *Schizodium* and *Disa* sect. *Micranthae*. Expansion cells, i.e. thin-walled cells on the adaxial side of the midrib thought to have a role in the movement of leaves in

Artificial key to subtribes and genera of Diseae (HK, PL)

1. • Dorsal sepal generally galeate and with an elongate or saccate spur, rarely spurless; lip linear, lorate, narrowly oblong or ovate 2
• Dorsal sepal rarely galeate and usually without spur; if spurred then with large lip appendage; lip various 4

2. • Lip narrowly lorate or linear, erect, shorter than the column; petals forming a hood together with the adnate dorsal sepal . . . .(**Subtribe Brownleeinae) 8. *Brownleea***
• Lip linear, lorate, ovate or rarely spathulate, occasionally lacerated on the margin, patent, exceeding the column in length; petals not adnate to the dorsal sepal galea, included in the galea at least basally . . . .(**Subtribe Disinae**) 3

3. • Lip with sac-like hypochile, flat mesochile, and tooth-like epichile; stems wiry and flexuose . . . .**15. *Schizodium***
• Lip not as above, lorate, linear, ovate, or spathulate, sometimes lacerate; stems erect and straight, or only slightly flexuose . . . .**14. *Disa***

4. • Lip basally united with the column, normally with an appendage mostly larger than the rest of the lip . . . .(**Subtribe Coryciinae**) 5
• Lip not united with the column, lacking an appendage 9

5. • Lateral sepals spurred or sacate . . . .**11. *Disperis***
• Lateral sepals not spurred or saccate 6

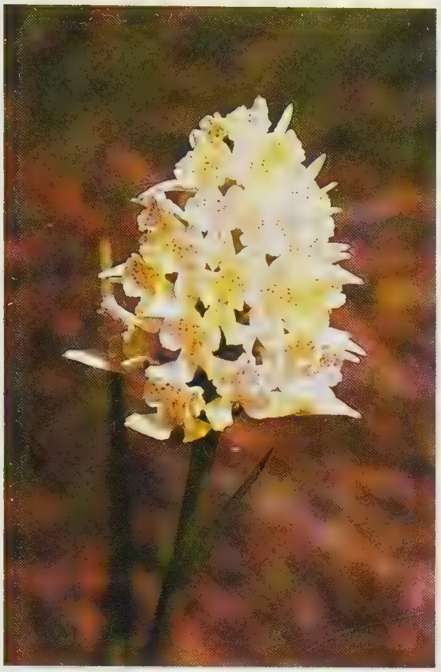
6. • Lip broadly triangular or anchor-shaped, with or without appendage 7
• Lip not broadly triangular or anchor-shaped, always with appendage 8

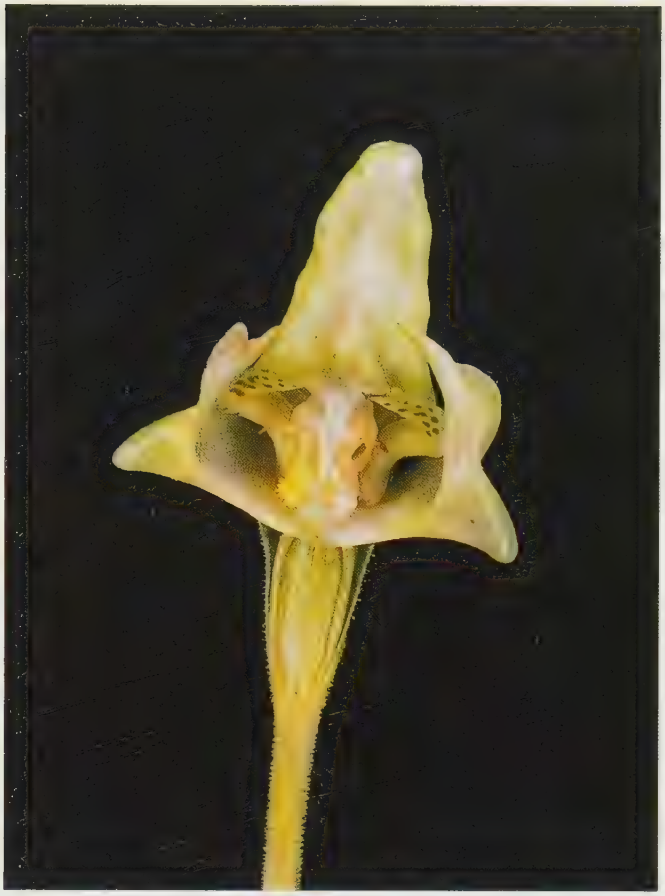
7. • Lip appendage either two-lobed or absent; lip blade with or without callus . . . .**9. *Ceratandra***
• Lip appendage unlobed; lip blade without a callus . . . .**12. *Evotella***

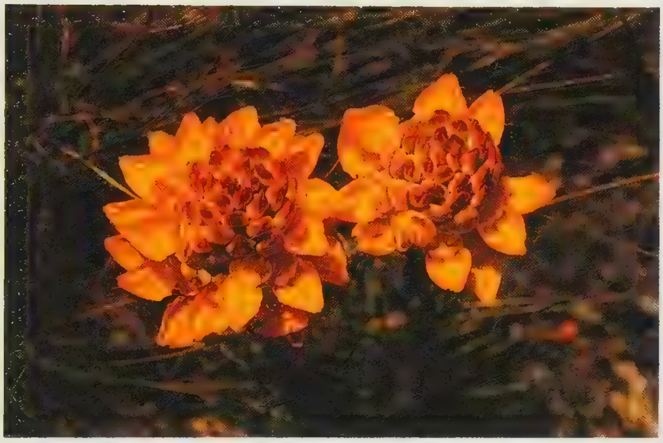
8. • Hood formed by the dorsal sepal and the petals shallow . . . .**13. *Pterygodium***
• Hood formed by the dorsal sepal and the petals deeply globose or subglobose . . . .**10. *Corycium***

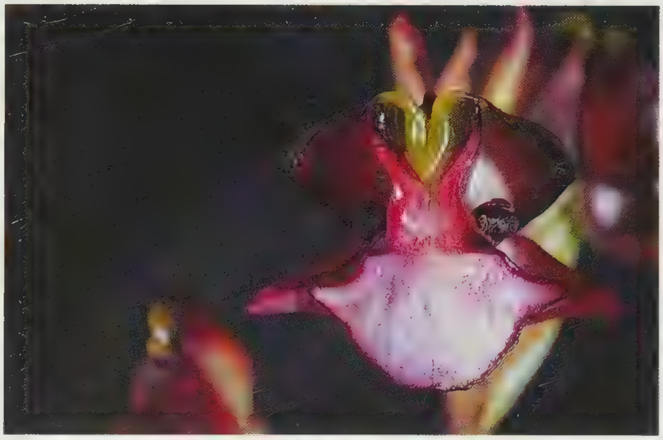
9. • Stalk of column absent; sepals and petals different; anther erect or suberect . . . .(**Subtribe Huttonaeinae**) **16. *Huttonaea***
• Stalk of the column prominent and longer than wide; flowers non-resupinate; sepals and petals similar and spreading; anther mostly pendent . . . .(**Subtribe Satyriinae**) 10

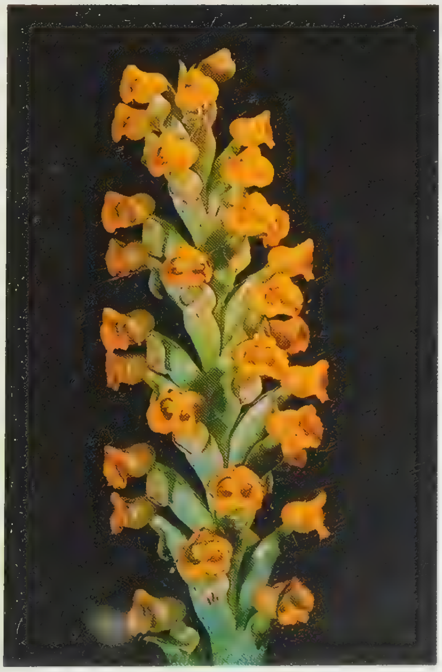
10. • Flowers zygomorphic; lip galeate and almost always with two spurs or sacs . . . .**18. *Satyrium***
• Flowers subactinomorphic; lip flat and unspurred . . . .**17. *Pachites***

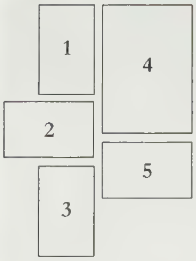












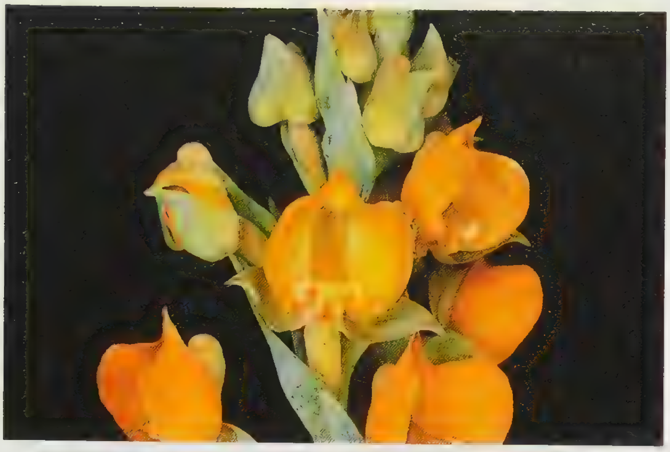
1 *Brownleea galpinii*, South Africa
(Photo: H. P. Linder)

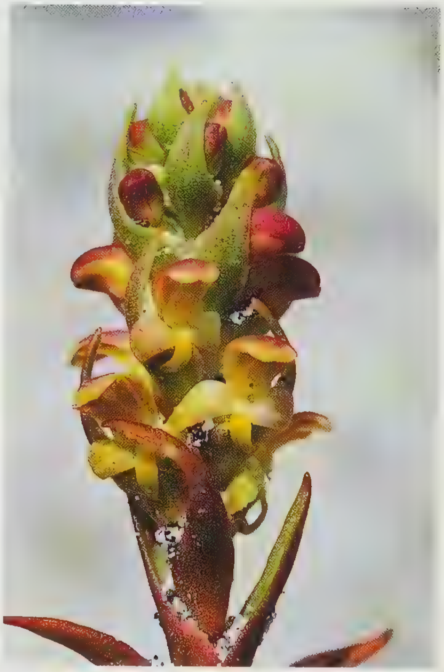
2 *Ceratandra grandiflora*, South Africa
(Photo: H. P. Linder)

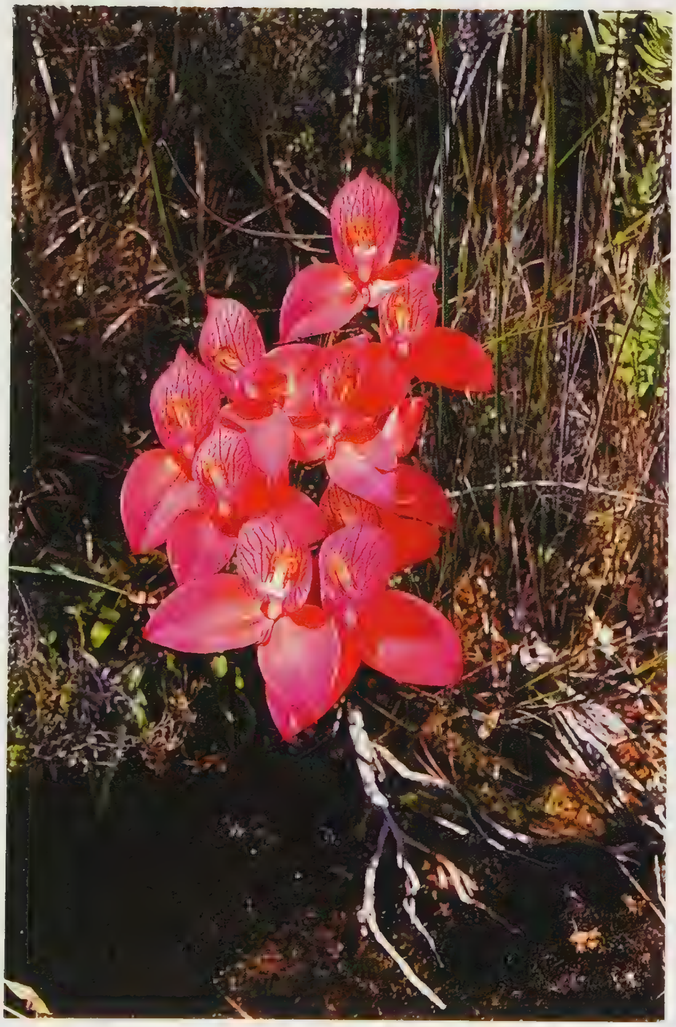
3 *Corycium crispum*, South Africa
(Photo: F. Duckitt)

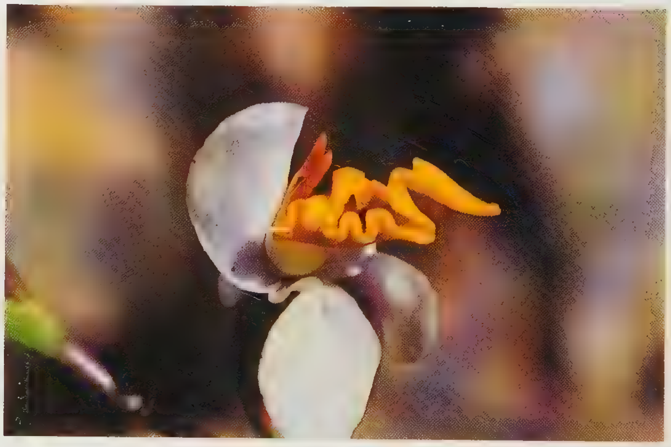
4 *Disperis cucullata*, South Africa
(Photo: F. Duckitt)

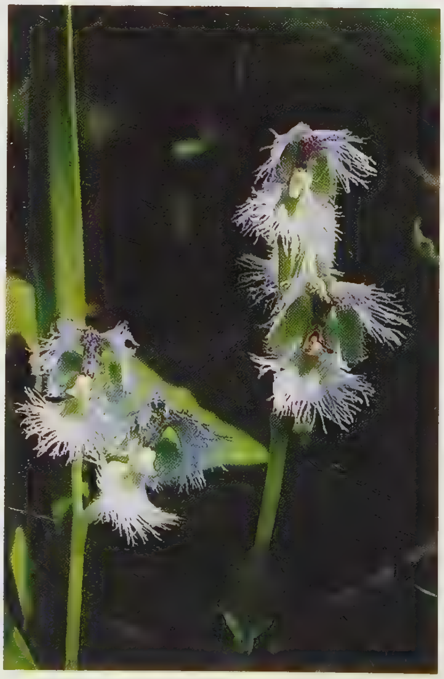
5 *Evotella rubiginosa*, South Africa
(Photo: H. Kurzweil)

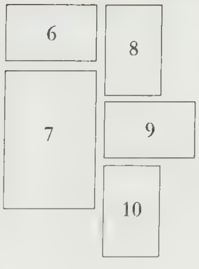












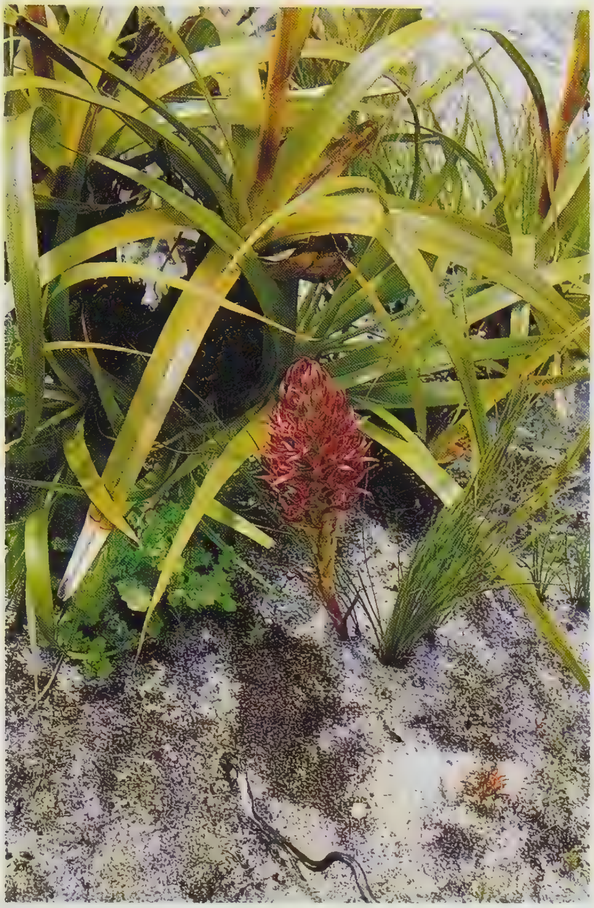
6 *Pterygodium acutifolium*, South Africa (Photo: F. Duckitt)

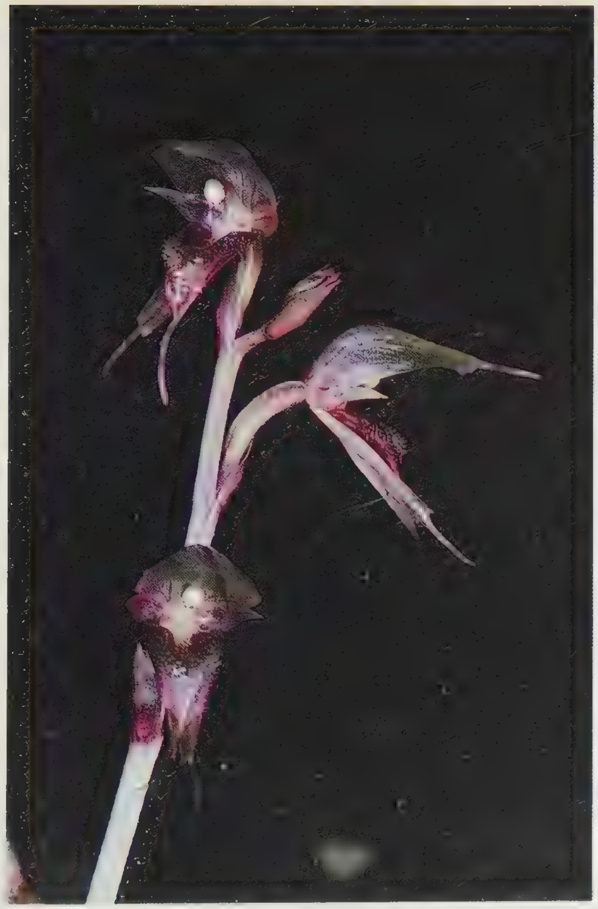
7 *Disa uniflora*, South Africa (Photo: L. Vogelpoel)

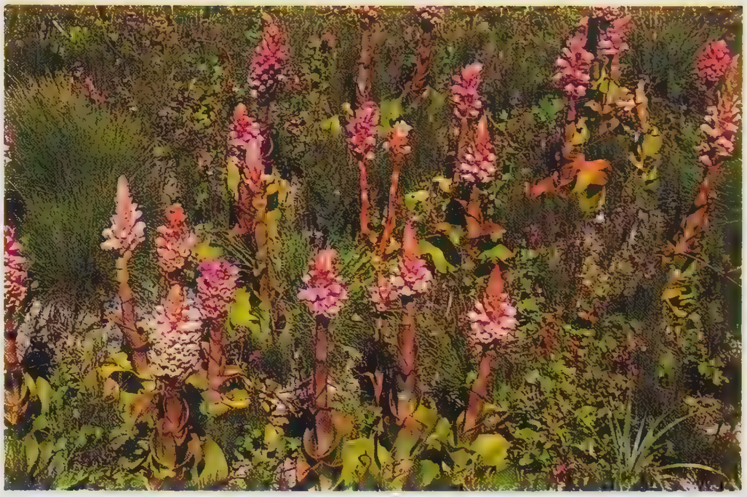
8 *Disa pygmaea*, South Africa (Photo: H. P. Linder)

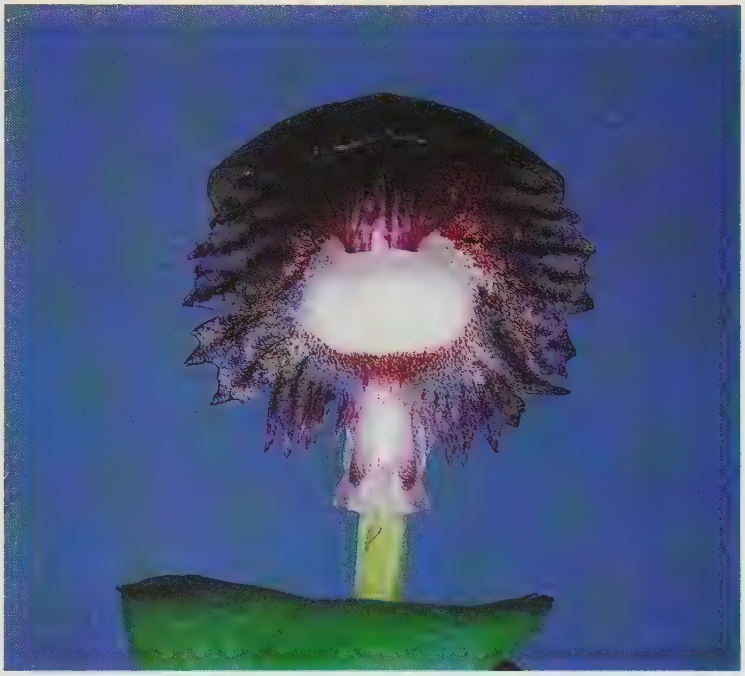
9 *Schizodium flexuosum*, South Africa (Photo: H. P. Linder)

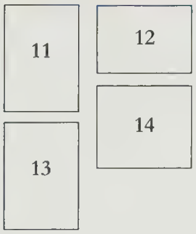
10 *Huttonaea grandiflora*, South Africa (Photo: J. Stewart)



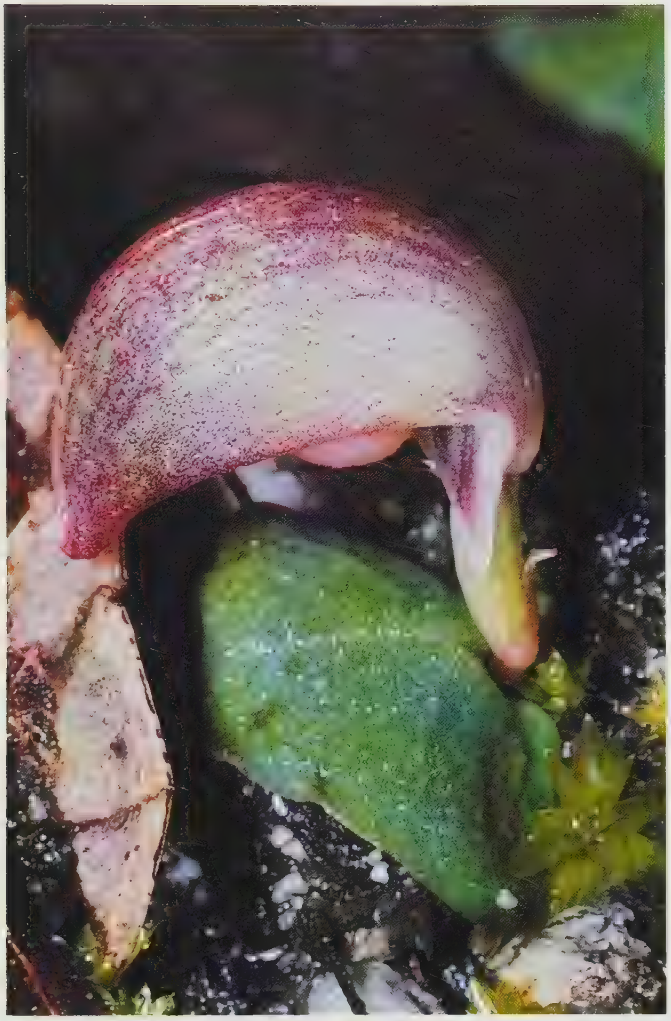


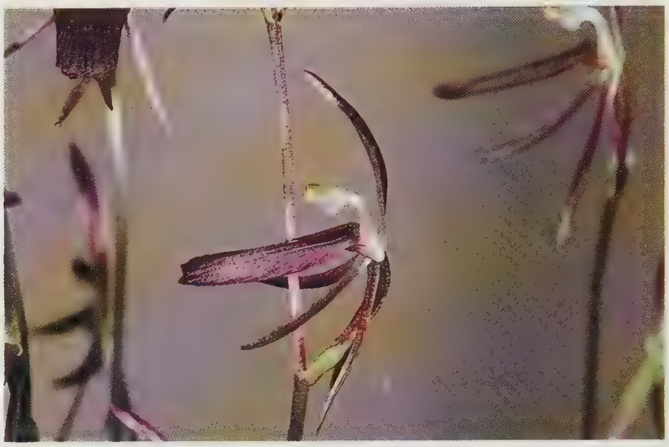


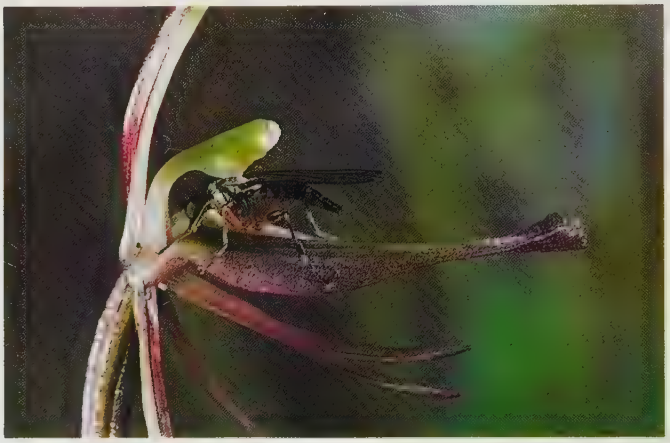


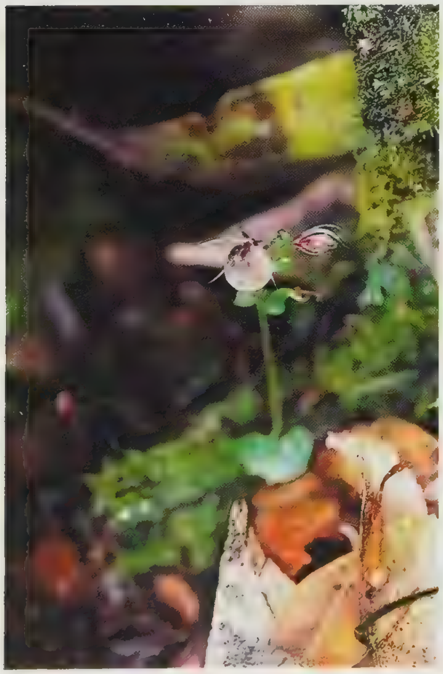


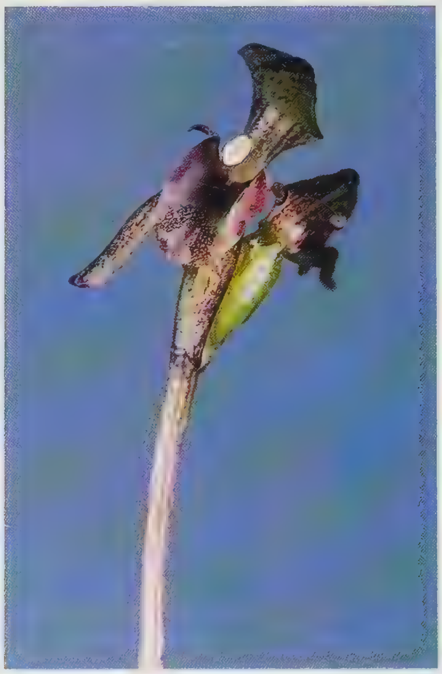
11 *Pachites bodkinii*, South Africa (Photo: H. Kurzweil)
12 *Satyrium carneum*, South Africa (Photo: L. Vogelpoel)
13 *Acianthus fornicatus*, Australia (Photo: M. A. Clements)
14 *Corybas dilatatus*, Australia (Photo: M. A. Clements)

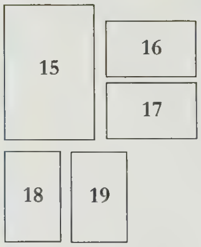












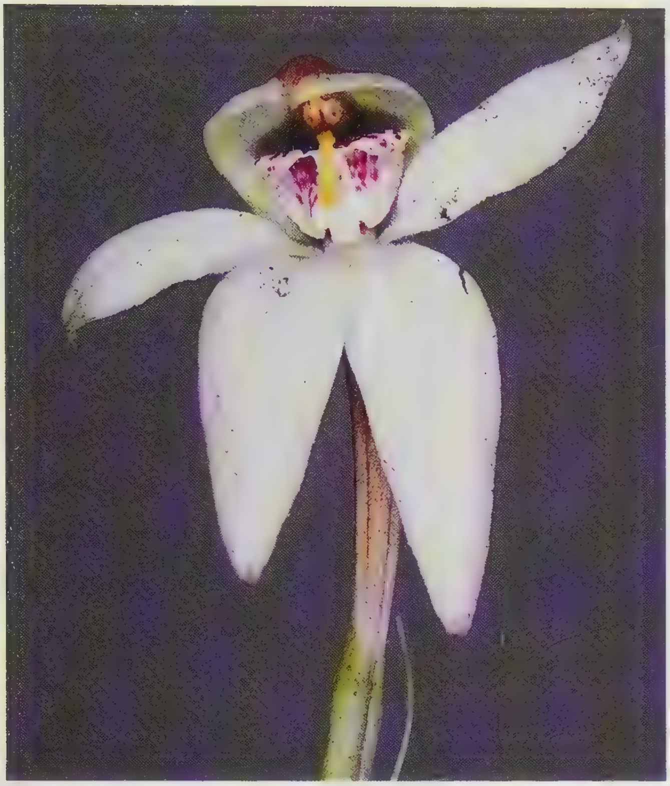
15 *Corybas aconitiflorus*, Australia (Photo: M. A. Clements)

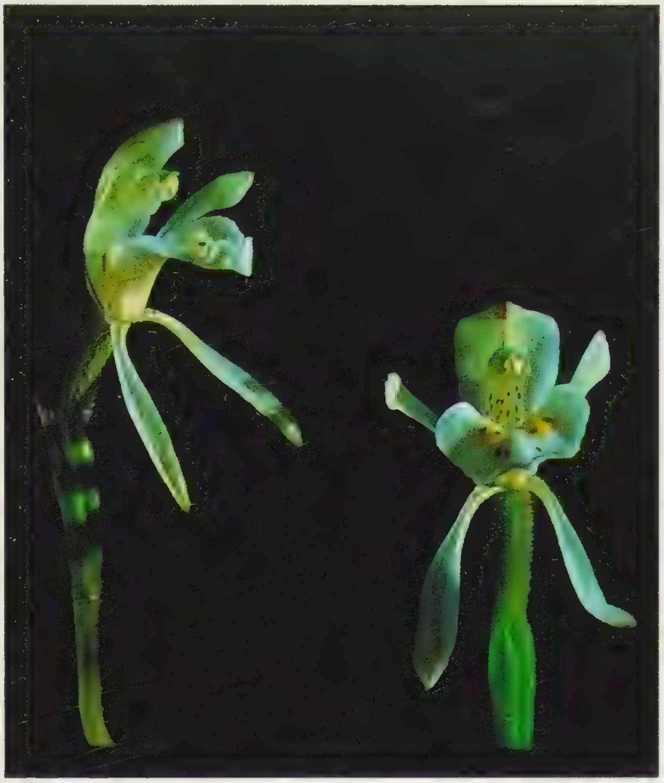
16 *Cyrtostylis reniformis*, Australia (Photo: M. A. Clements)

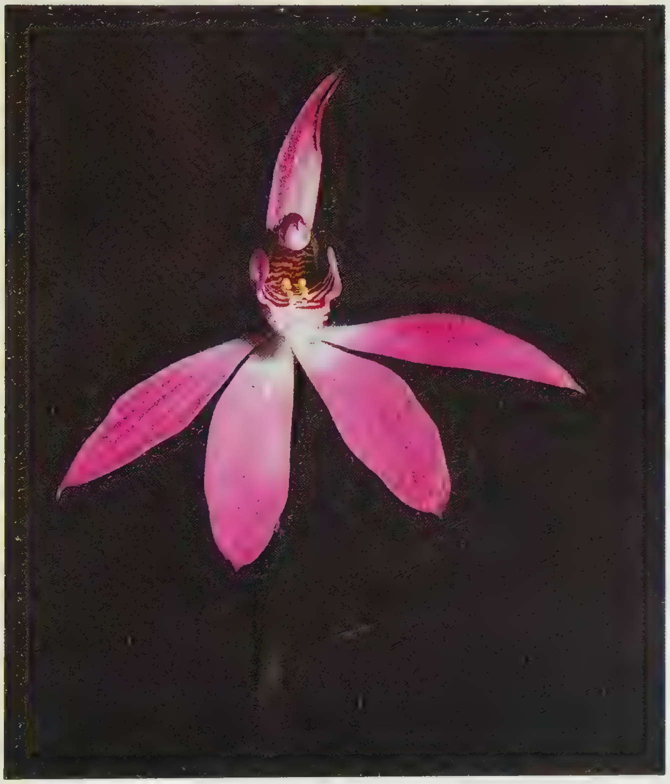
17 An empidid fly, *Atrichopleura* sp. imbibing nectar on the labellum of *Cyrtostylis reniformis*. Note the pollinia on its thorax between the column wings. Australia (Photo: C. C. Bower)

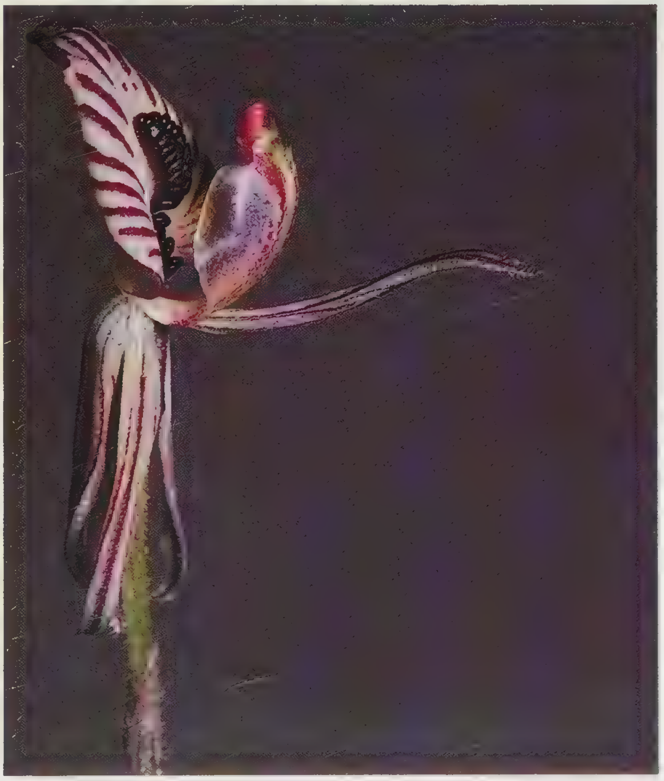
18 *Stigmatodactylus vulcanicus*, Papua New Guinea (Photo: M. A. Clements)

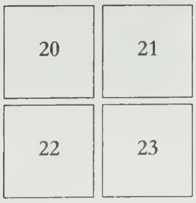
19 *Townsonia viridis*, Australia (Photo: M. A. Clements)









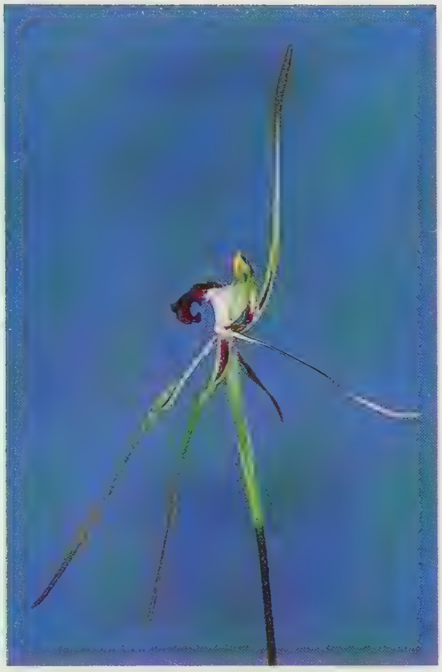


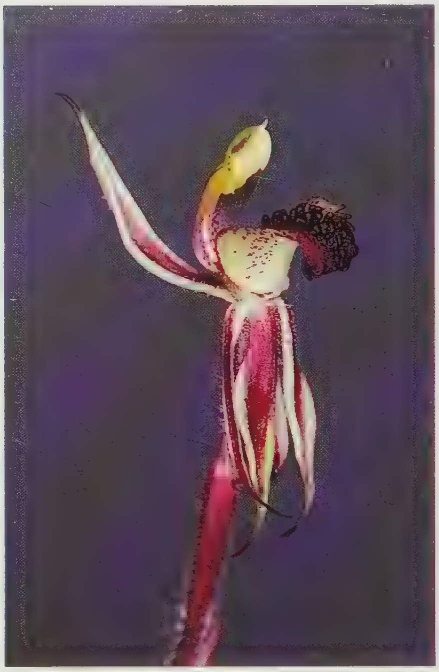
20 *Adenochilus nortonii*, Australia (Photo: M. A. Clements)

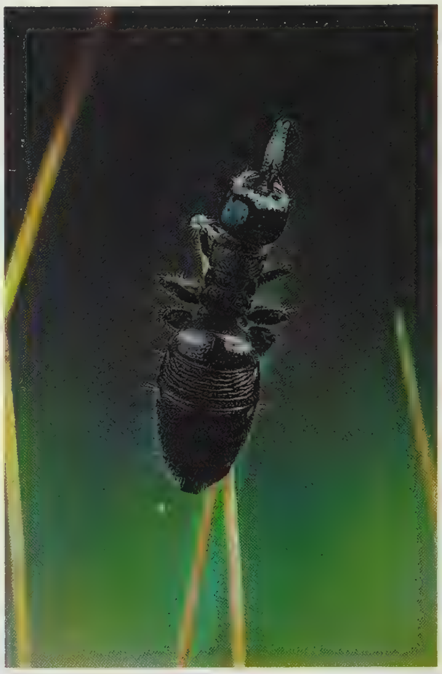
21 *Aporostylis bifolia*, New Zealand (Photo: J. H. G. Johns)

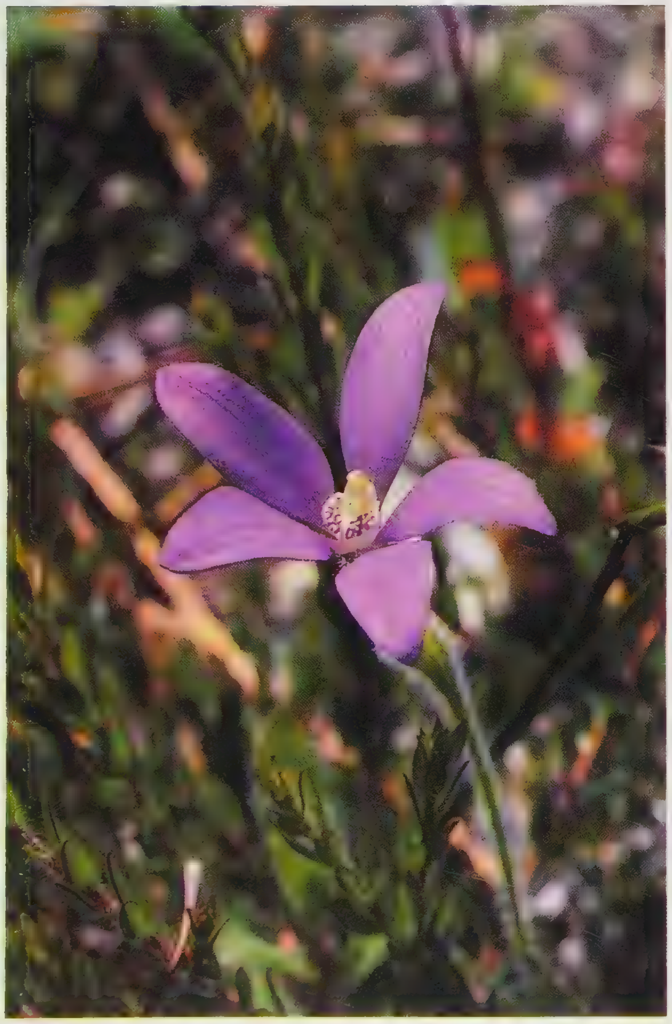
22 *Caladenia carnea*, Australia (Photo: M. A. Clements)

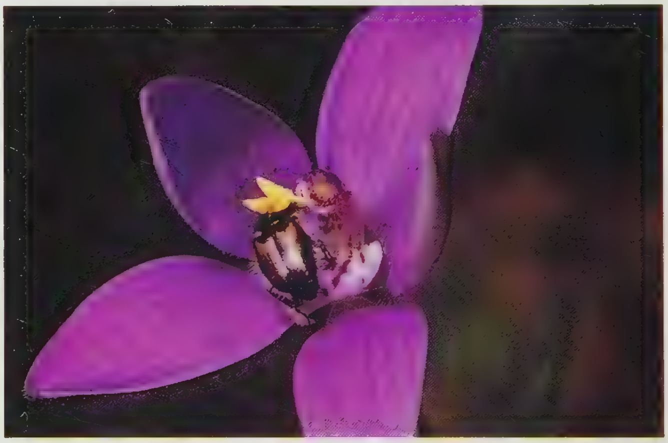
23 *Caladenia cairnsiana*, Australia (Photo: M. A. Clements)

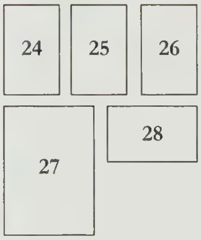












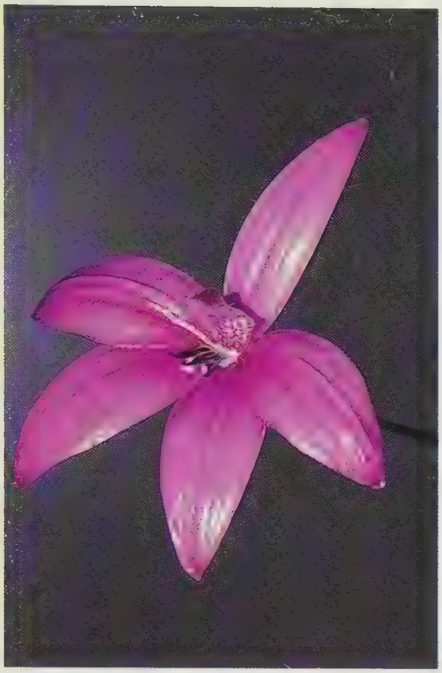
24 *Caladenia dilatata*, Australia (Photo: M. A. Clements)

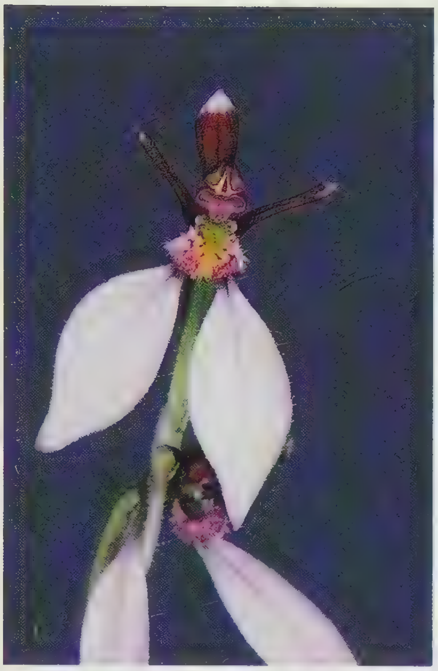
25 *Caladenia actensis*, Australia (Photo: M. A. Clements)

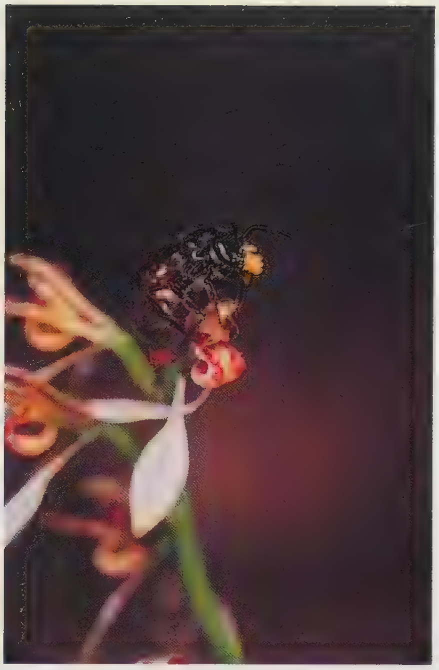
26 A typical flightless female thynnine wasp as mimicked by all Drakaeinae and some Caladeniinae. The female is in the calling position on a grass stem. Australia (Photo: C. C. Bower)

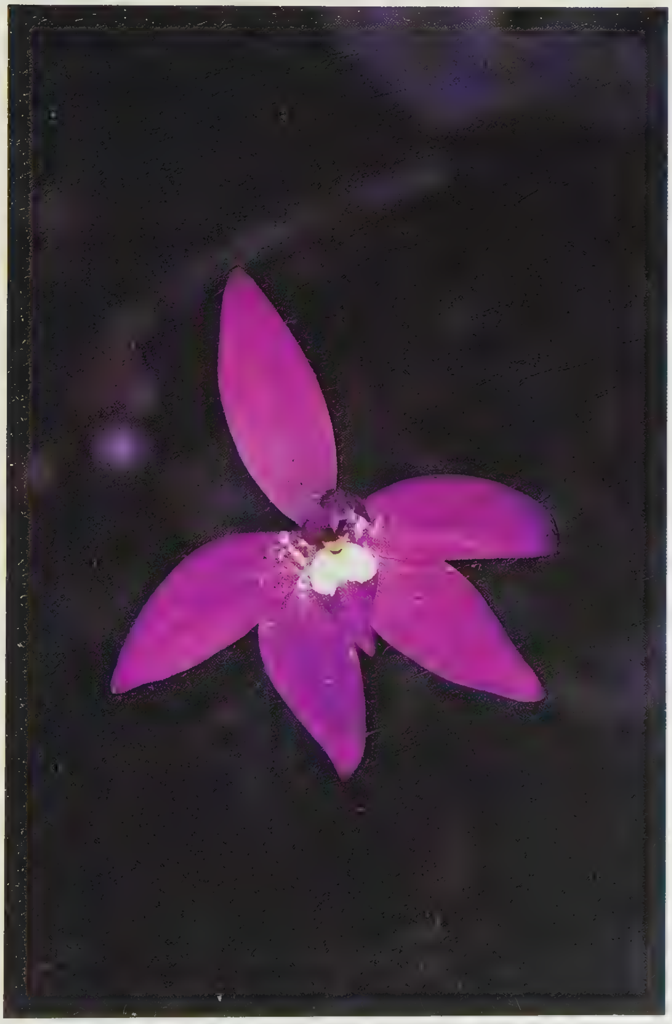
27 *Cyanicula gemmata*, Australia (Photo: M. Rohlach)

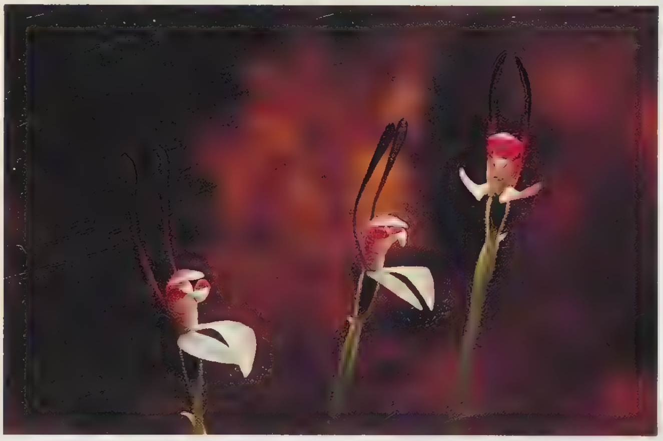
28 Nectar scarab, *Neophyllotocus* sp., with pollinia on a flower of *Cyanicula gemmata*, Australia (Photo: R. Peakall)

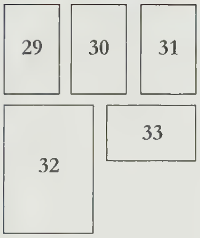












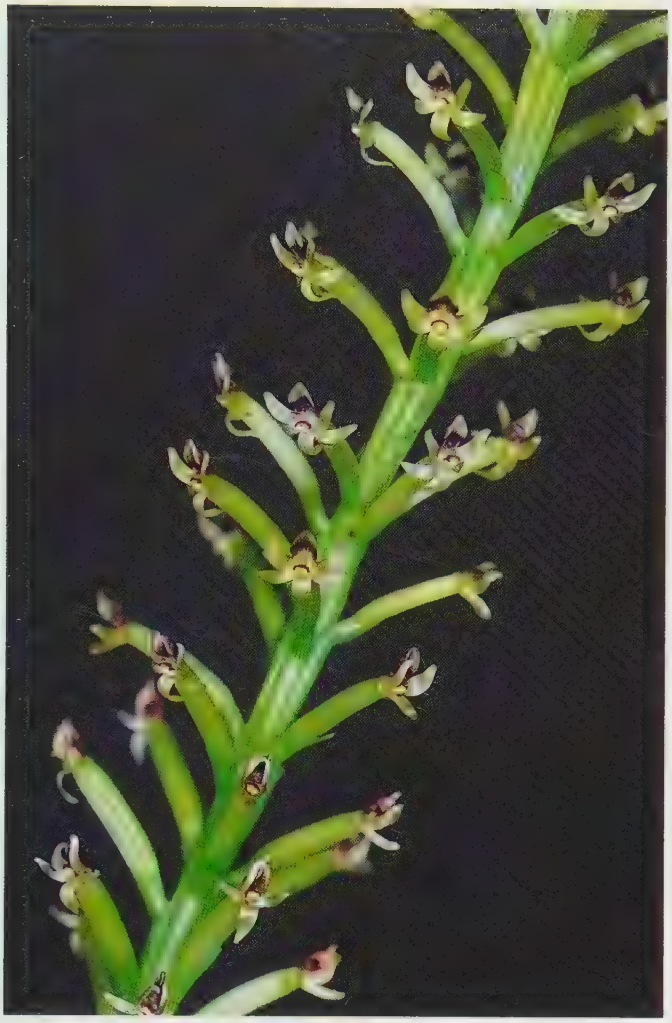
29 *Elythranthera emarginata*, Australia (Photo: M. A. Clements)

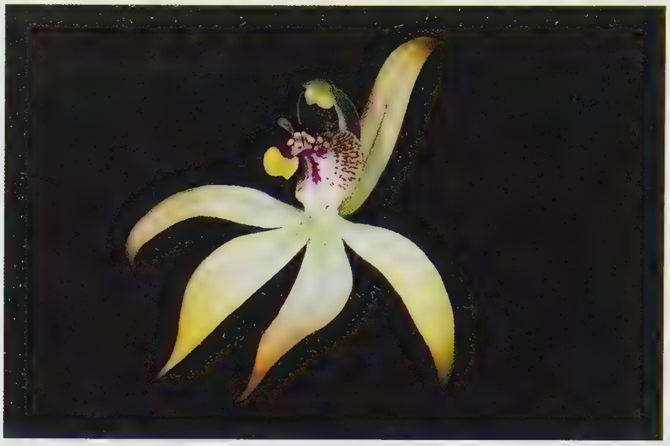
30 *Eriochilus cucullatus*, Australia (Photo: M. A. Clements)

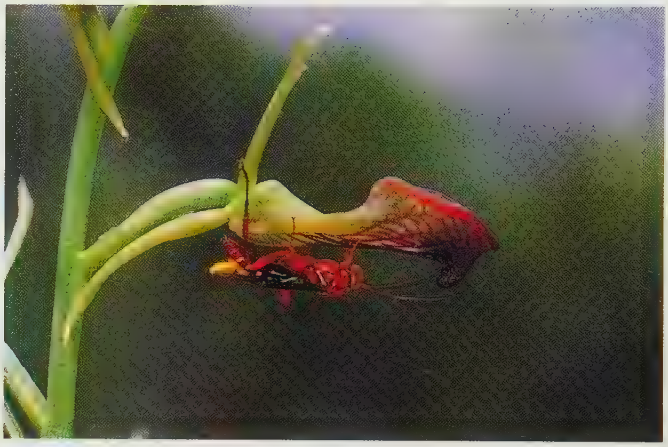
31 Unidentified native bee bearing pollinia on a flower of *Eriochilus dilatatus*, Australia (Photo: R. Peakall)

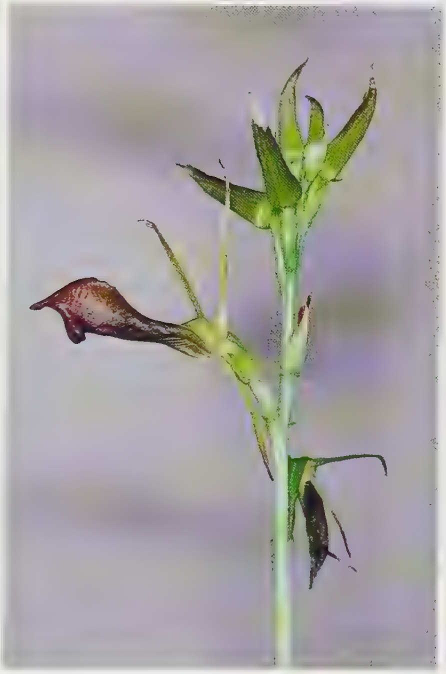
32 *Glossodia major*, Australia (Photo: M. A. Clements)

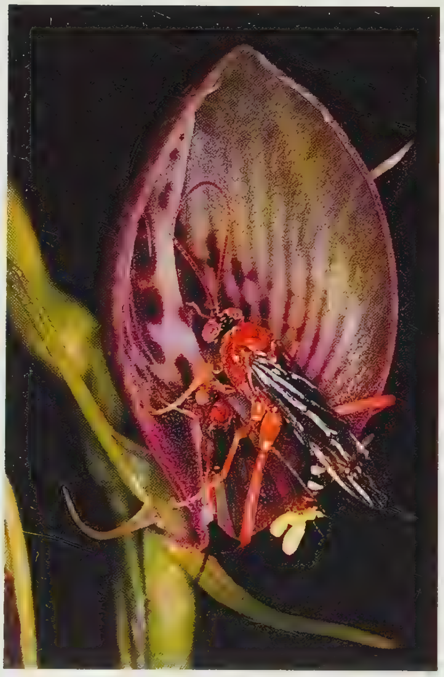
33 *Leptoceras menziesii*, Australia (Photo: M. Rohlach)

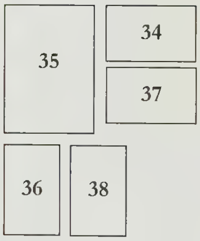












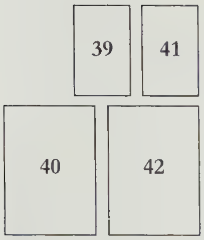
34 *Praecoxanthus aphyllus*, Australia (Photo: M. A. Clements)

35 *Coilochilus neocaledonicus*, New Caledonia (Photo: M. A. Clements)

36 *Cryptostylis ovata*, Australia (Photo: M. A. Clements)

37 Male ichneumonid wasp, *Lissopimpla excelsa*, with pollinarium on *Cryptostylis ovata*, Australia (Photo: R. Peakall)

38 *Cryptostylis erecta*, Australia (Photo: M. Rohlach)

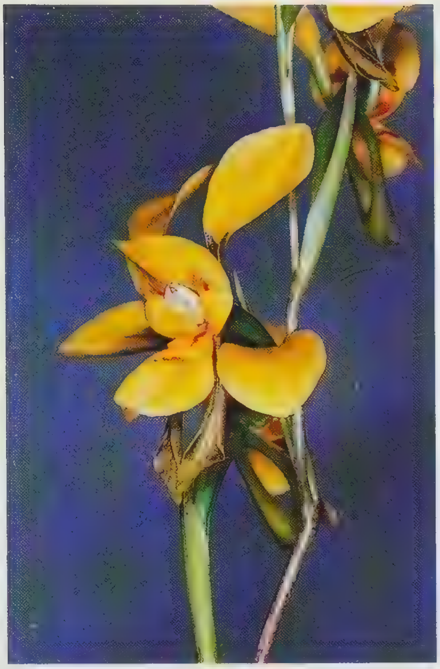


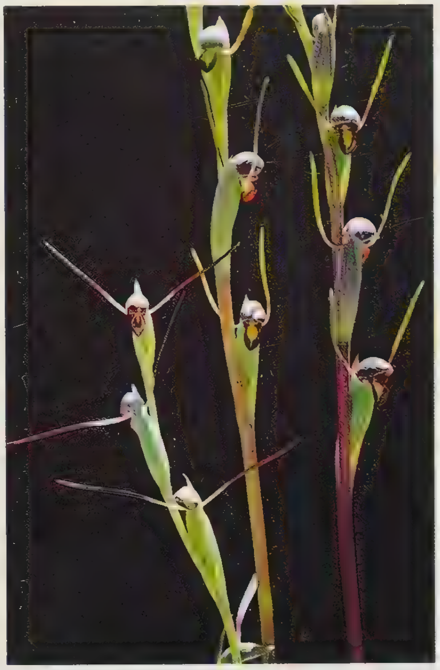
39 *Diuris aurea*, Australia
(Photo: M. A. Clements)

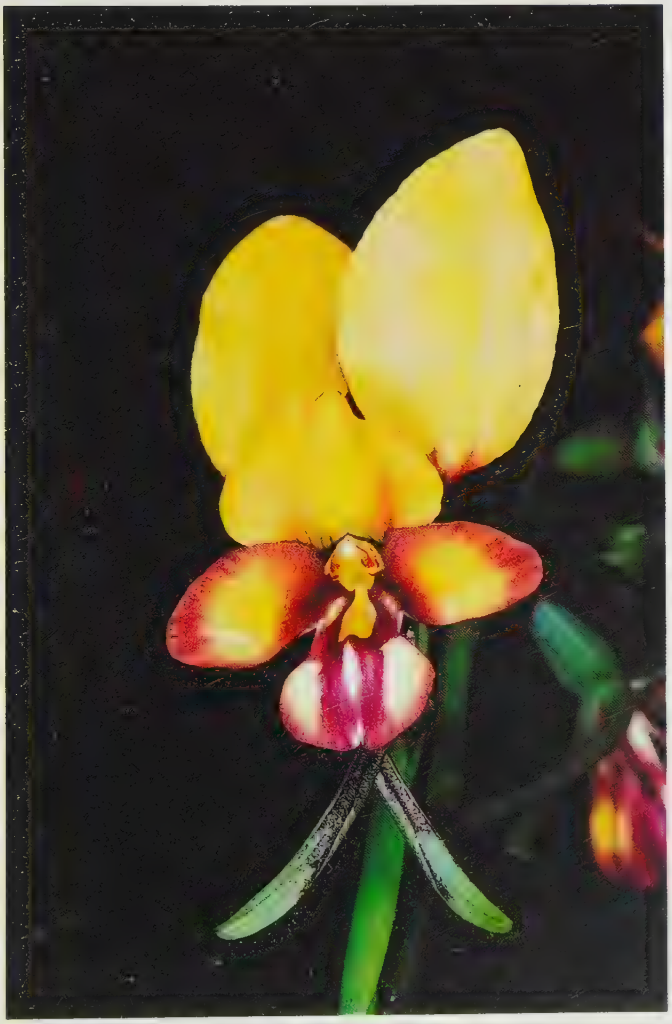
40 *Diuris magnifica*, Australia
(Photo: M. A. Clements)

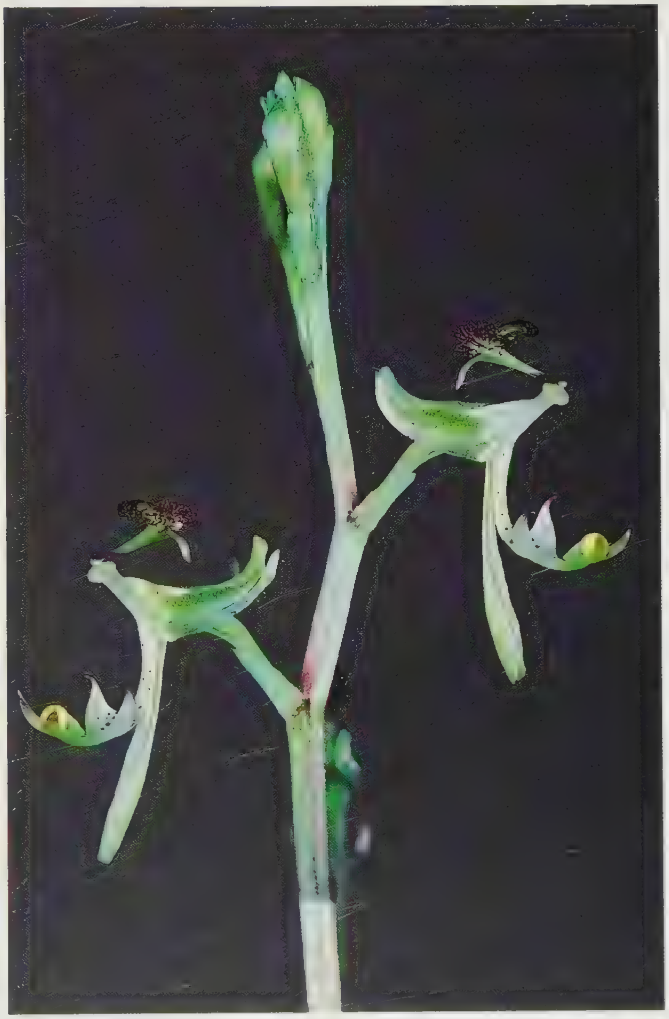
41 *Orthoceras strictum*, Australia
(Photo: M. A. Clements)

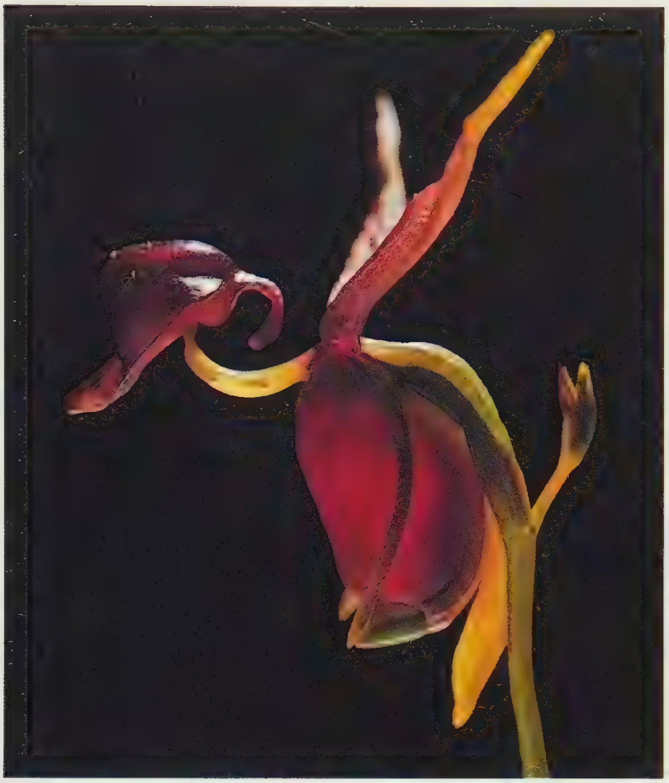
42 *Arthrochilus irritabilis*, Australia
(Photo: M. A. Clements)

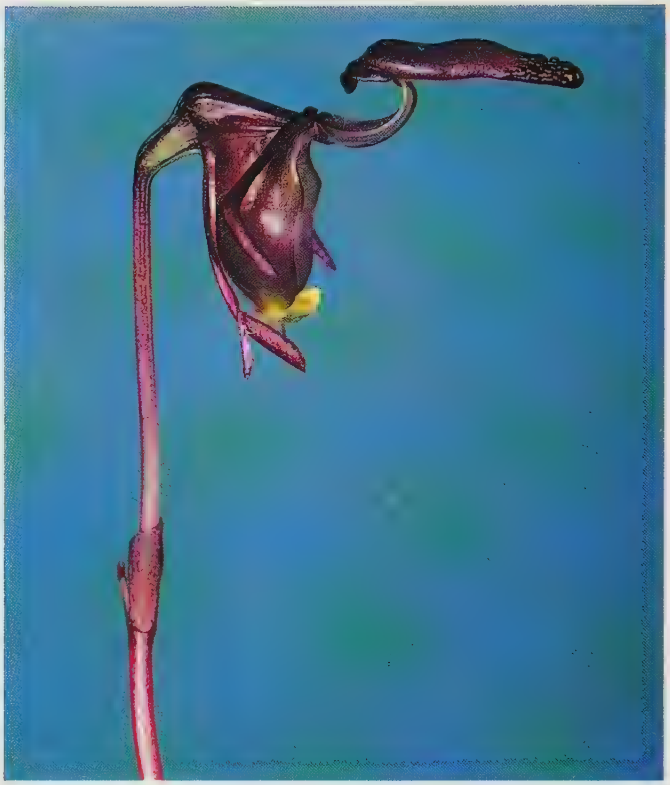


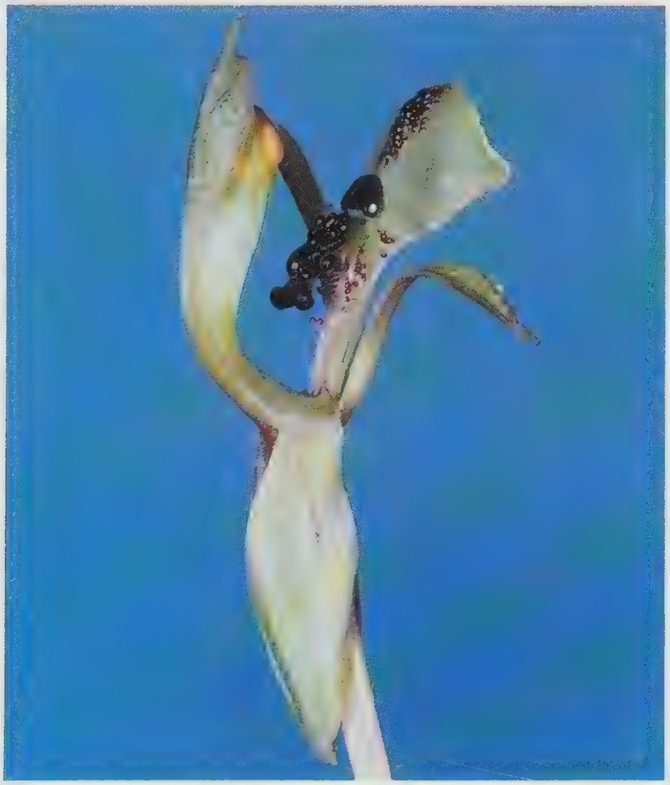


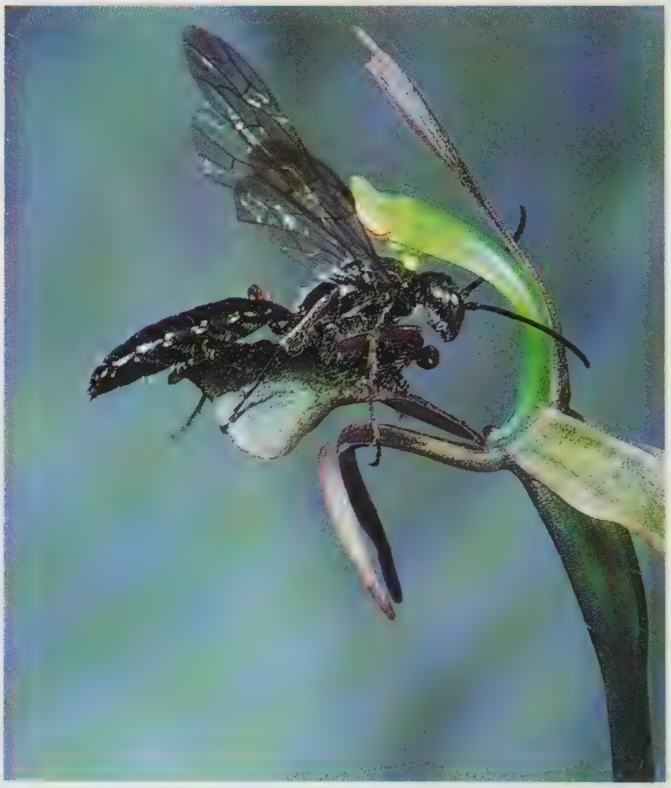












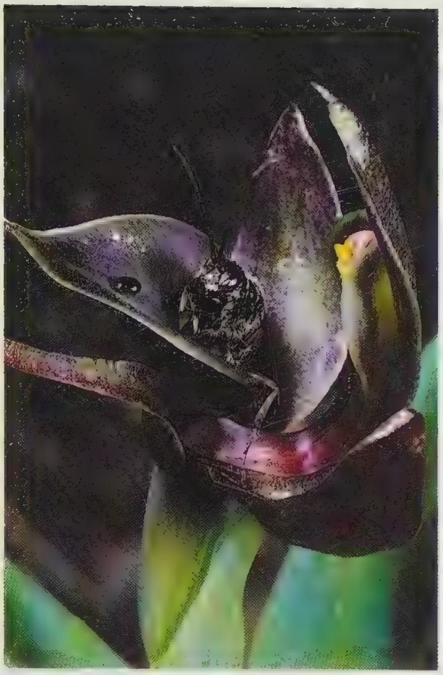
43	44
45	46

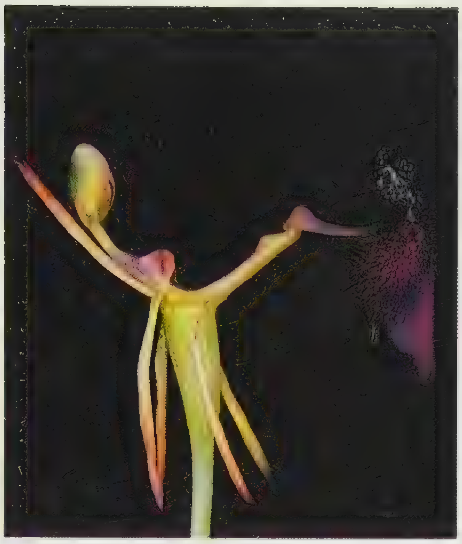
43 *Caleana major*, Australia (Photo: M. Rohlach)

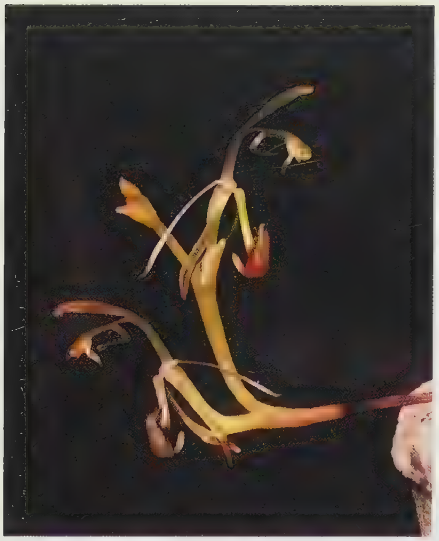
44 *Caleana nigrita*, Australia (Photo: M. A. Clements)

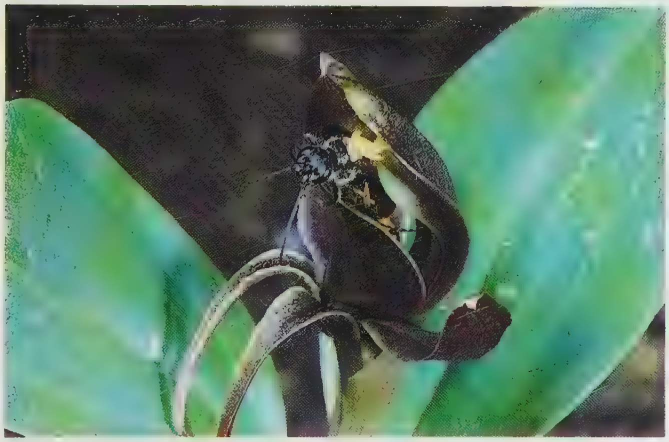
45 *Chiloglottis fornicatus*, Australia (Photo: M. A. Clements)

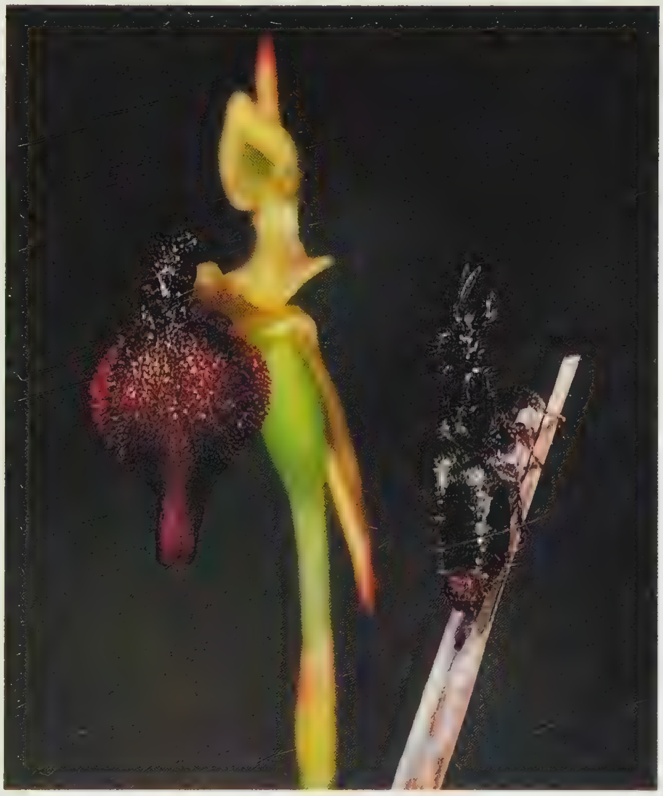
46 Male thynnine wasp, *Neozeloboria* sp., grappling with the thorax of the pseudofemale decoy of *Chiloglottis formicifera* with its forelegs, Australia (Photo: C. C. Bower)

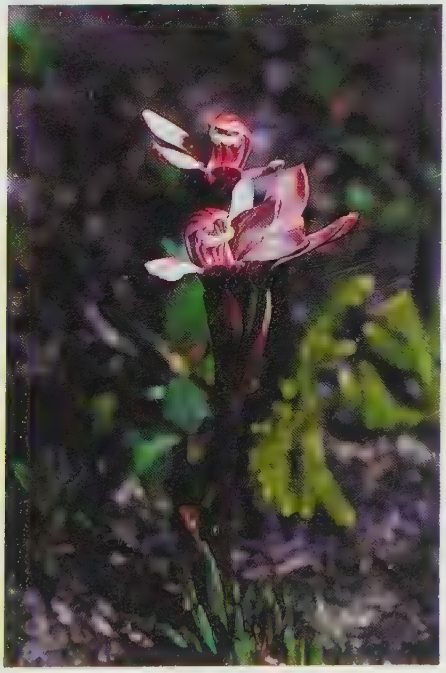


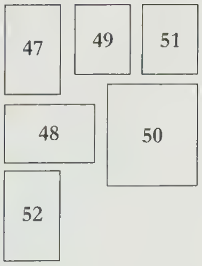












47 Male *Neozeloboria monticola* clasping the central basal callus of *Chiloglottis valida* just below its slightly enlarged apex, Australia (Photo: C. C. Bower)

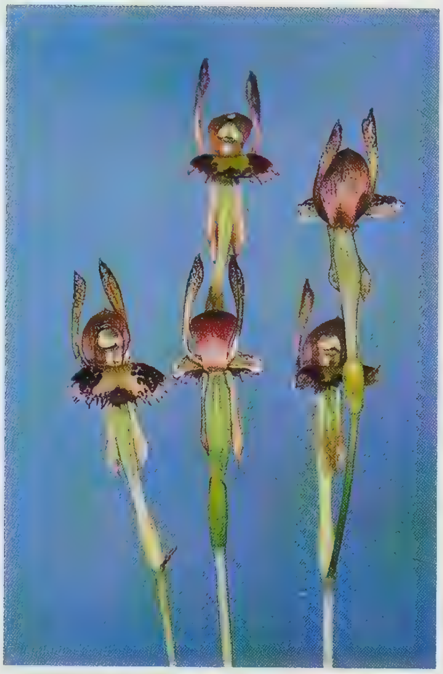
48 Male *Neozeloboria monticola* emerging with pollinia on its thorax from between the tipped labellum and column of *Chiloglottis valida*, Australia (Photo: C. C. Bower)

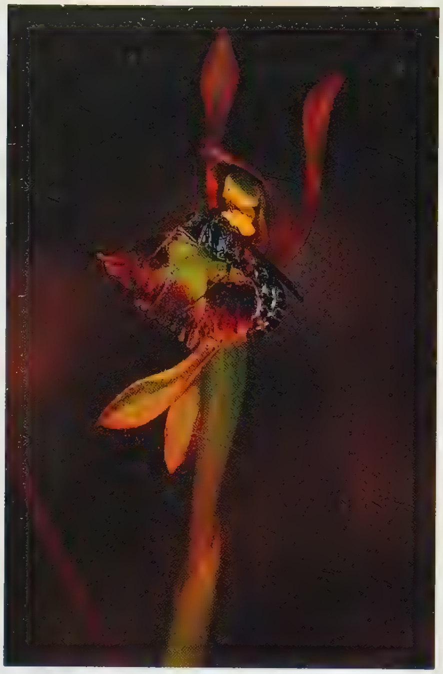
49 *Drakaea glyptodon*, Australia (Photo: M. A. Clements)

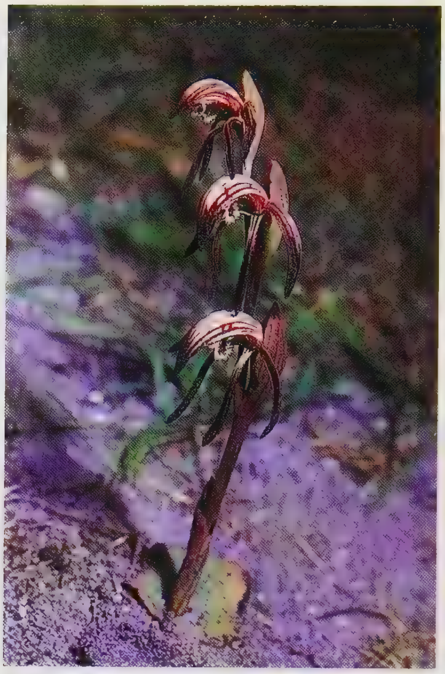
50 Comparison of the female thynnine wasp *Zaspilothynnus trilobatus* and the orchid which mimics it, *Drakaea glyptodon*, Australia (Photo: R. Peakall)

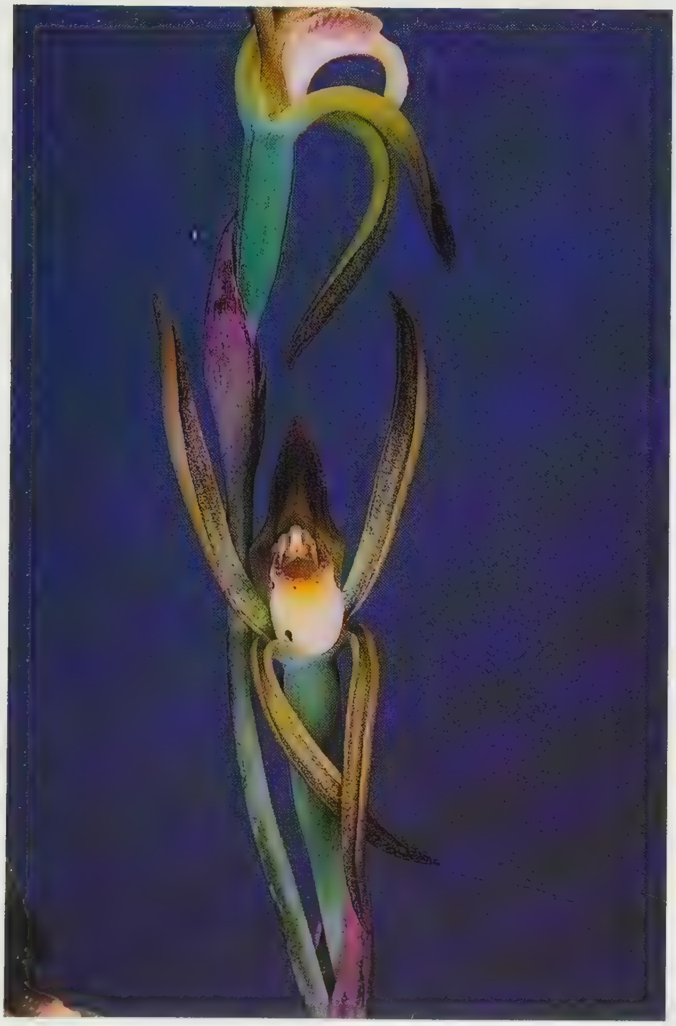
51 *Spiculaea ciliata*, Australia (Photo: M. A. Clements)

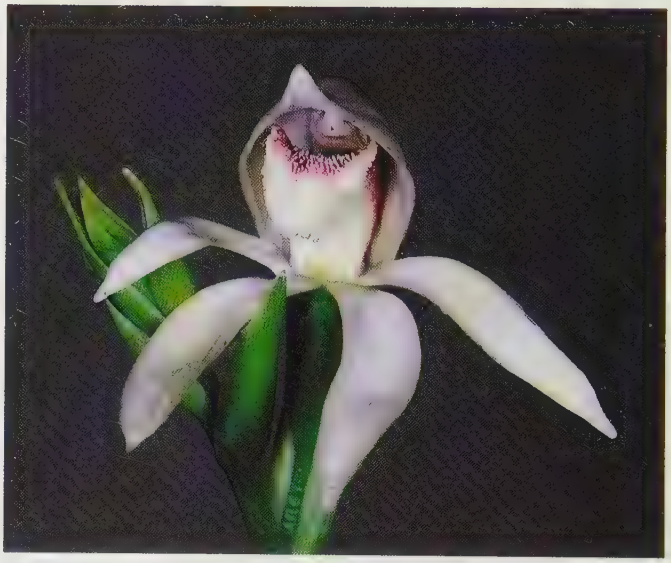
52 *Burnettia cuneata*, Australia (Photo: J. Johnson)

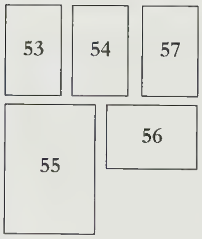












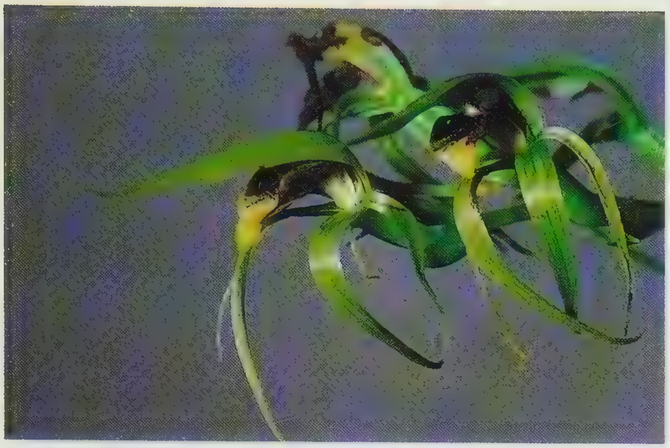
53 *Leporella fimbriata*, Australia (Photo: M. A. Clements)

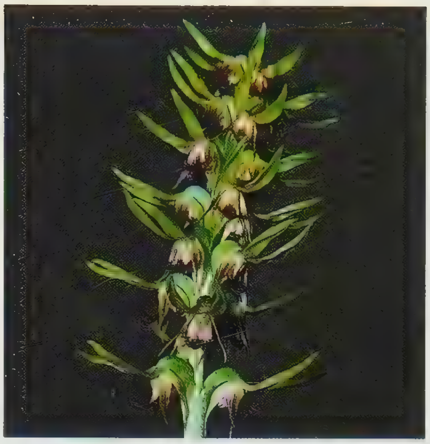
54 Male ant, *Myrmecia urens*, with pollinia on its thorax, pseudocopulating on the labellum of *Leporella fimbriata*, Australia (Photo: R. Peakall)

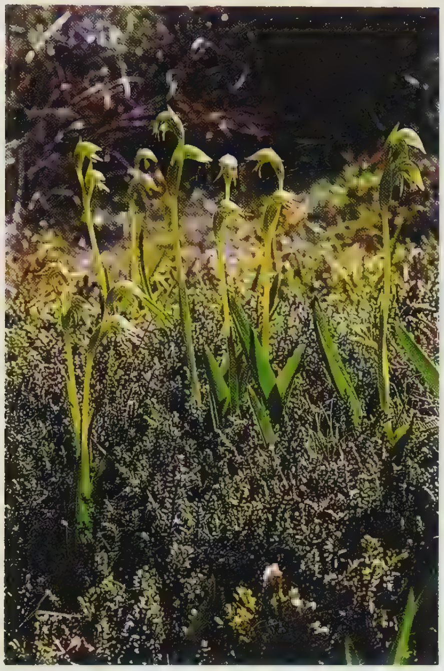
55 *Lyperanthus suaveolens*, Australia (Photo: M. A. Clements)

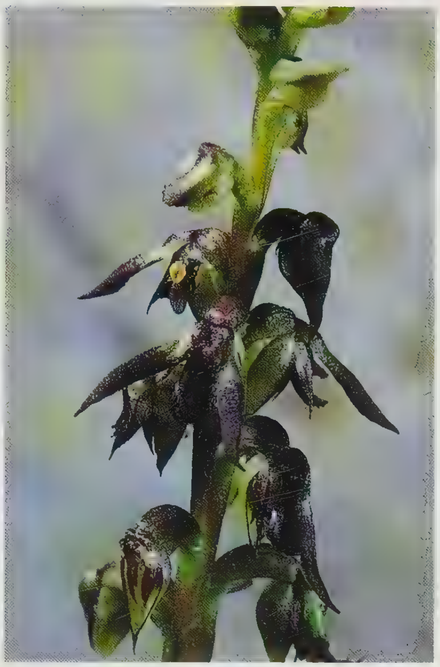
56 *Megastylis gigas*, New Caledonia (Photo: M. A. Clements)

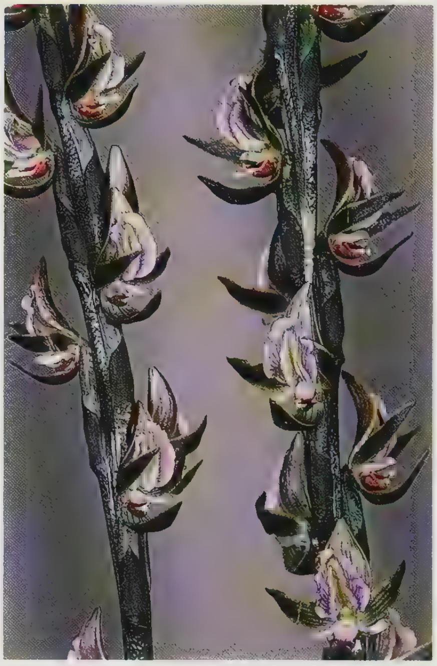
57 *Pyrorchis nigricans*, Australia (Photo: J. Johnson)

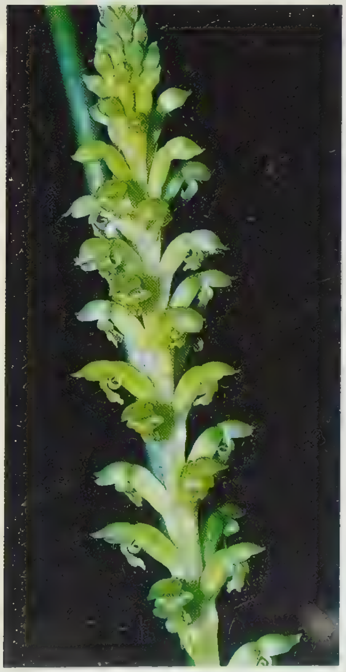


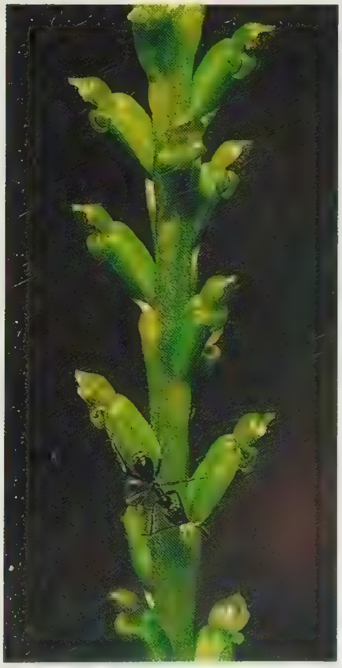


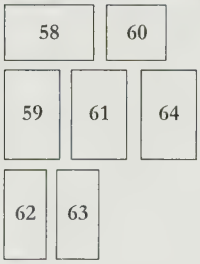












58 *Rimacola elliptica*, Australia, (Photo: M. A. Clements)

59 *Waireia stenopetala*, New Zealand (Photo: J. H. G. Johns)

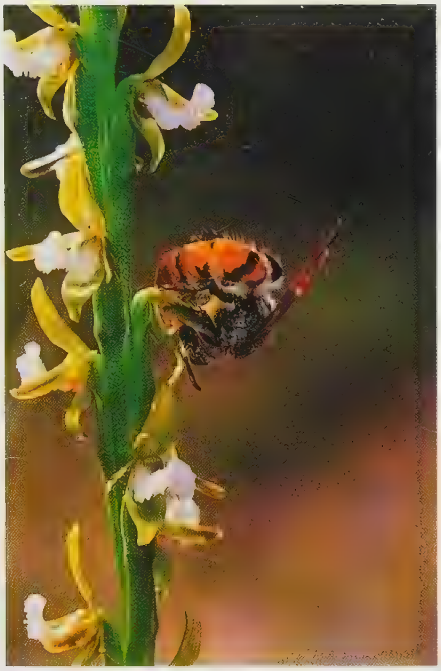
60 *Genoplesium sagittiferum*, Australia (Photo: M. A. Clements)

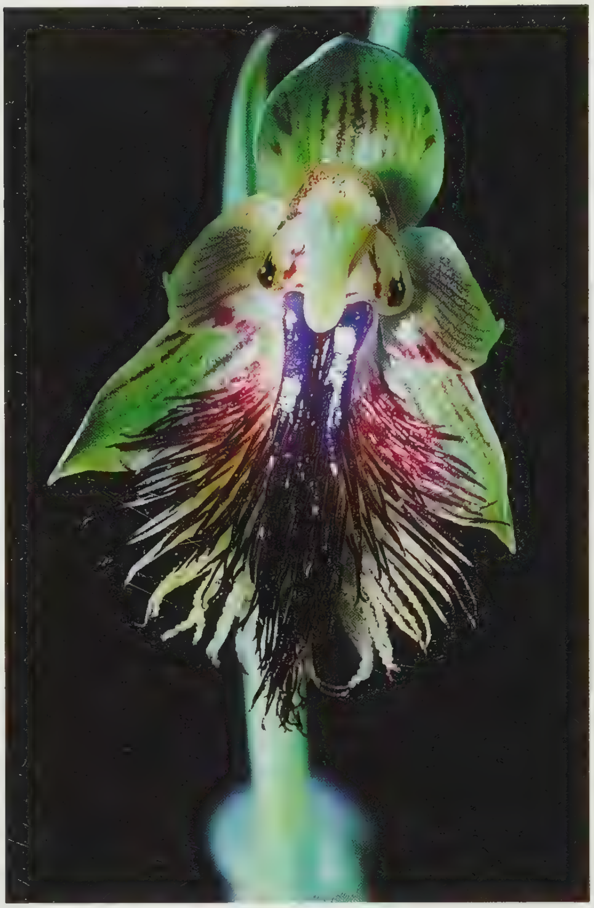
61 A chloropid fly with a pollinarium of an undescribed species of *Genoplesium* on its thorax, Australia (Photo: C. C. Bower)

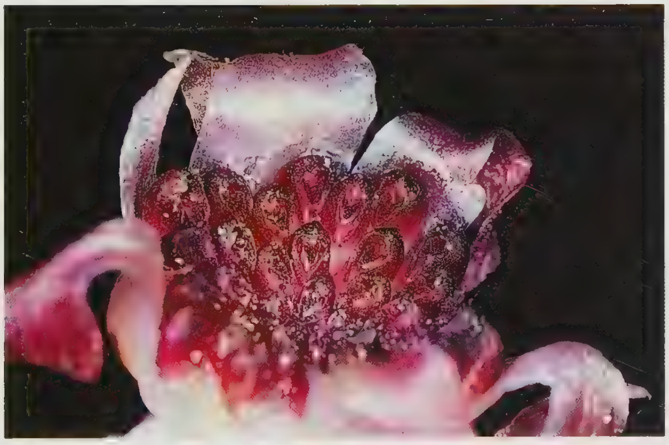
62 *Microtis media*, Australia (Photo: M. A. Clements)

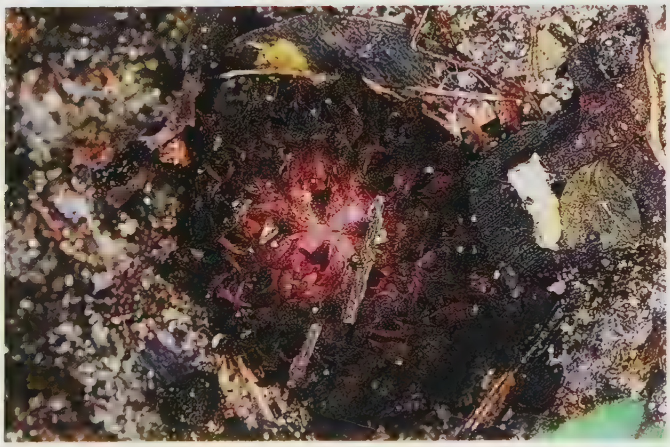
63 An *Iridomyrmex gracilis* worker ant with a pollinarium of *Microtis parviflora* attached to its frons, Australia (Photo: R. Peakall)

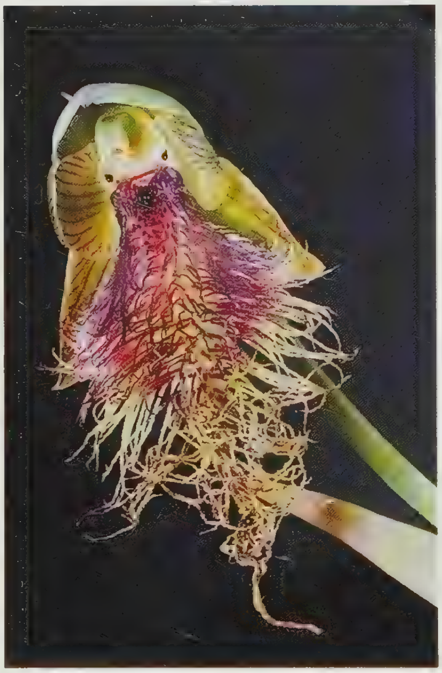
64 *Prasophyllum giganteum*, Australia (Photo: M. A. Clements)











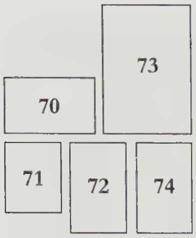
65 Unidentified native wasp adopting the head-downward feeding position on the labellum of *Prasophyllum fimbria*, Australia (Photo: R. Peakall)

66 *Rhizanthella gardneri*, Australia (Photo: M. A. Clements)

67 *Rhizanthella slateri*, Australia (Photo: M. A. Clements)

68 *Calochilus campestris*, Australia (Photo: M. A. Clements)

69 *Calochilus robertsonii*, Australia (Photo: M. A. Clements)



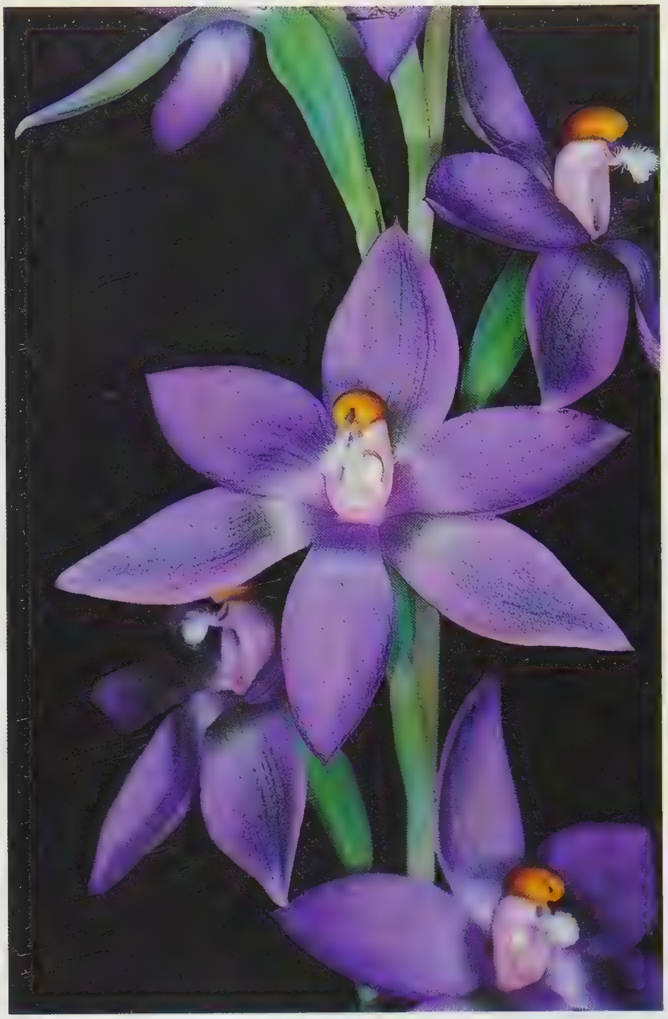
70 *Epiblema grandiflorum*, Australia (Photo: M. A. Clements)

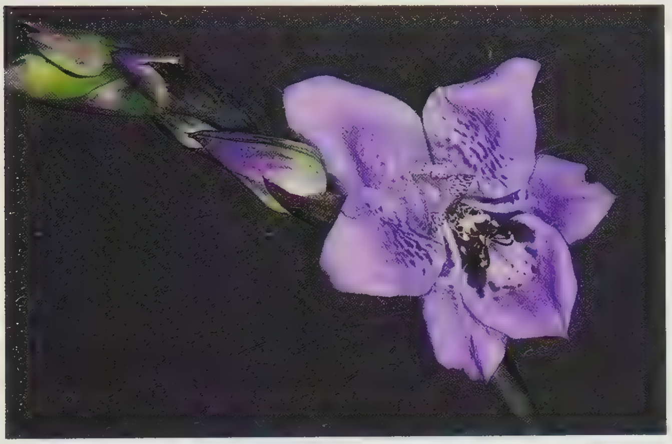
71 *Thelymitra apiculata*, Australia (Photo: M. A. Clements)

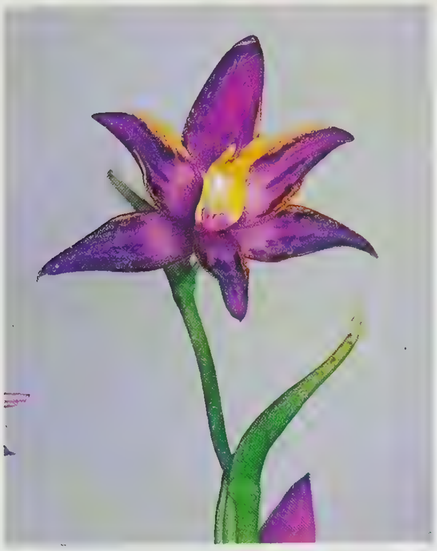
72 *Thelymitra dedmanae*, Australia (Photo: M. A. Clements)

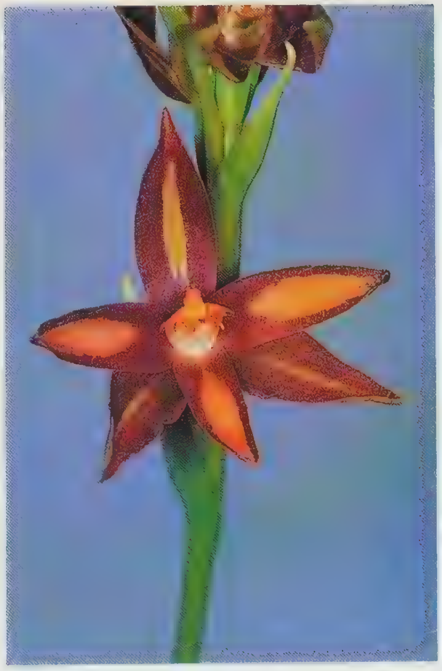
73 *Thelymitra megcalyptra*, Australia (Photo: M. A. Clements)

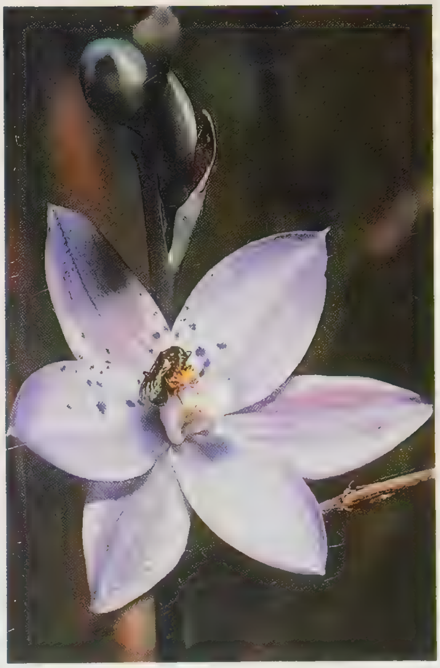
74 Unidentified native bee attempting to scrape pollen from the post-anther lobe on the column hood of *Thelymitra ixioides*, Australia (Photo: R. Peakall)

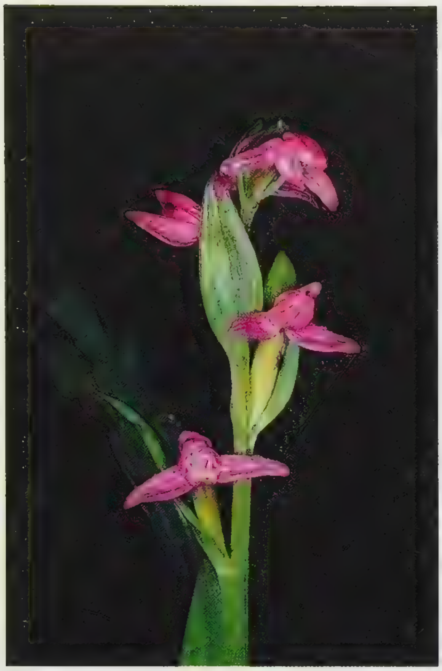


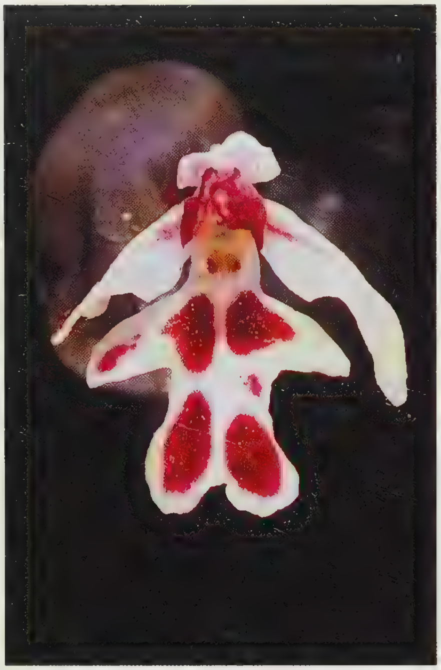


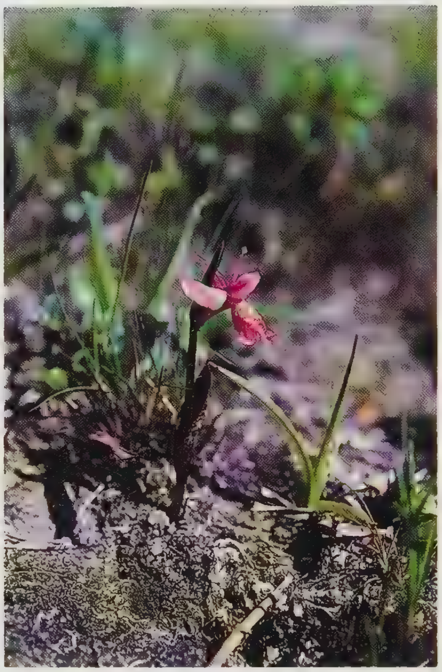


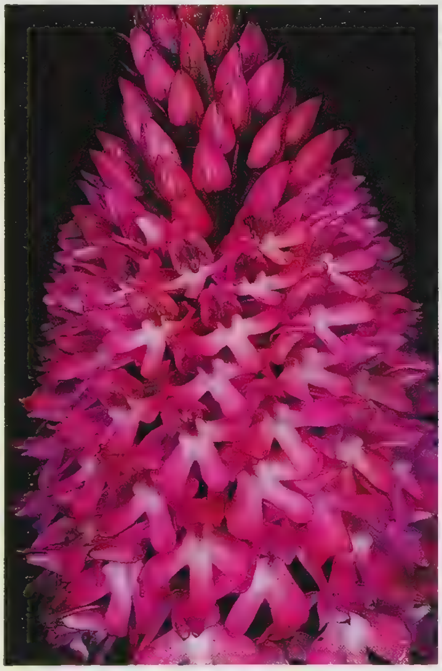


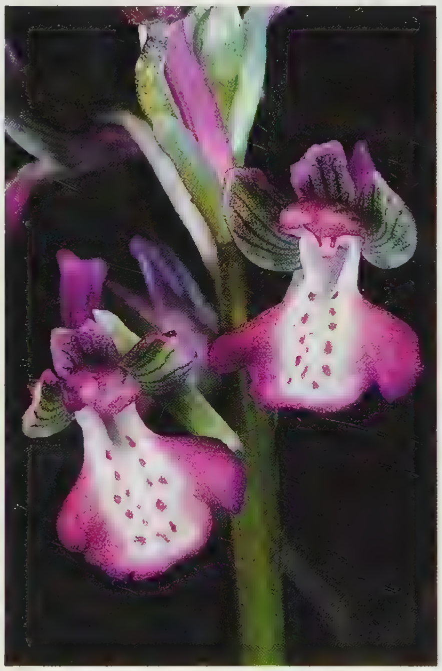


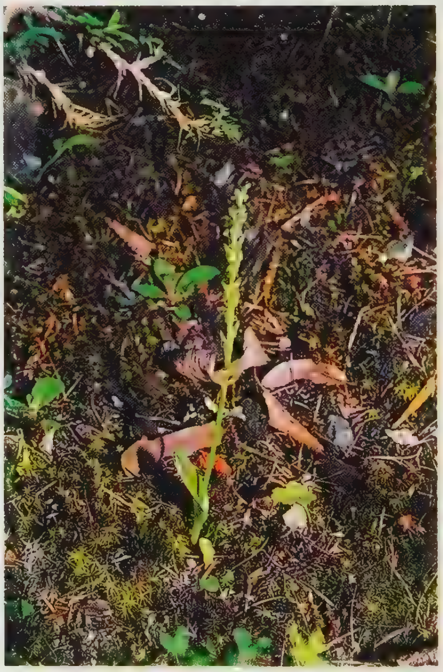












75	76	77
78	79	80

75 *Aceratorchis tschiliensis,* China (Photo: P. Cribb)

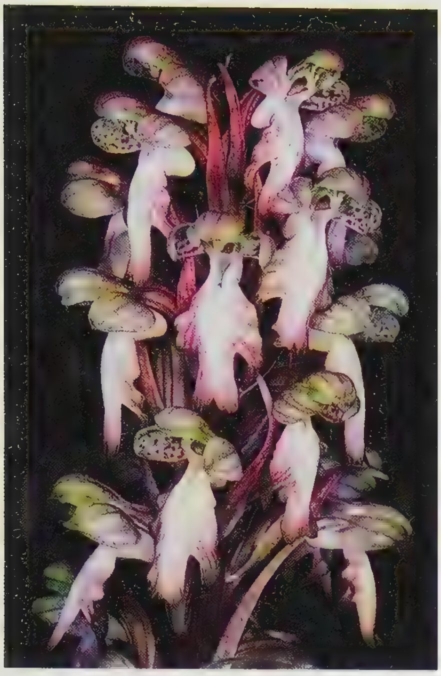
76 *Amerorchis rotundifolia*, Canada (Photo: M. MacConaill)

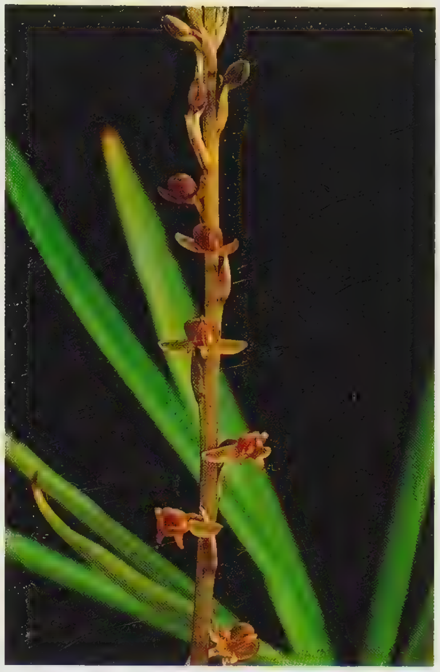
77 *Amitostigma tibeticum*, Tibet (Photo: P. Cribb)

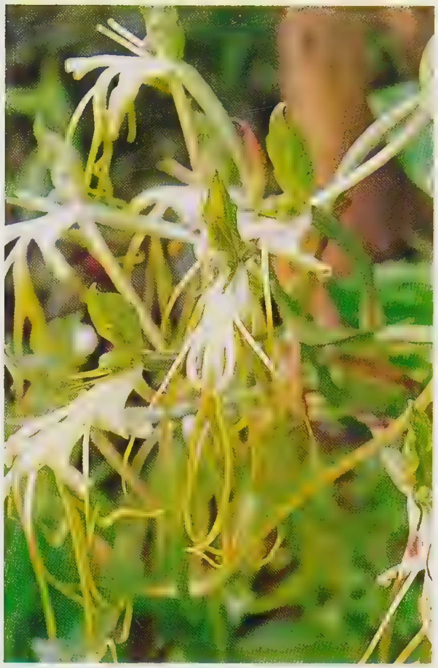
78 *Anacamptis pyramidalis*, United Kingdom (Photo: P. Gasson)

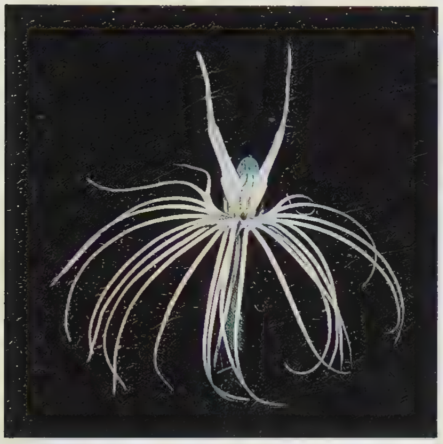
79 *Anacamptis morio* subsp. *picta*, United Kingdom (Photo: P. H. Davies)

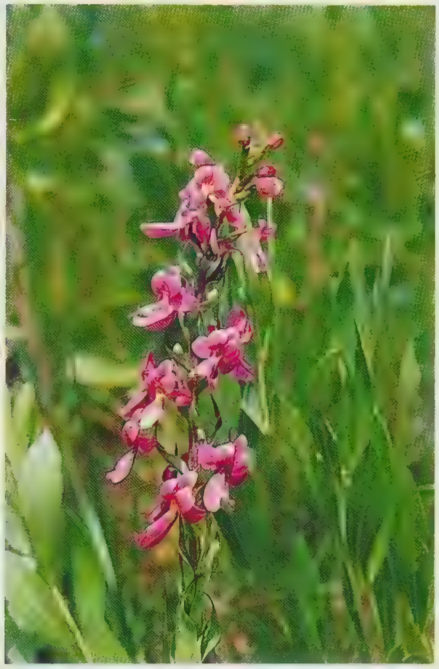
80 *Androcorys ophioglossoides*, China (Photo: P. Cribb)

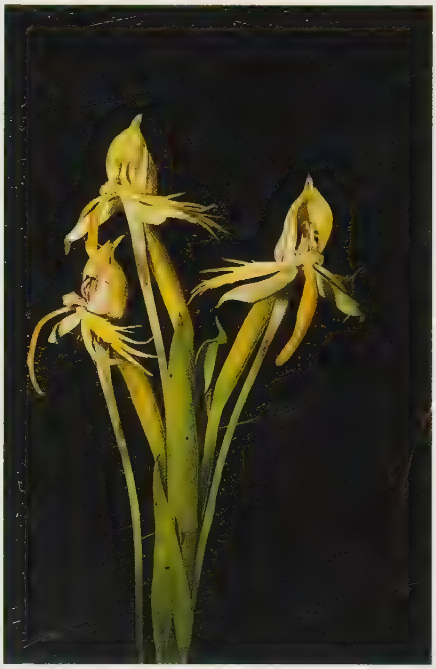


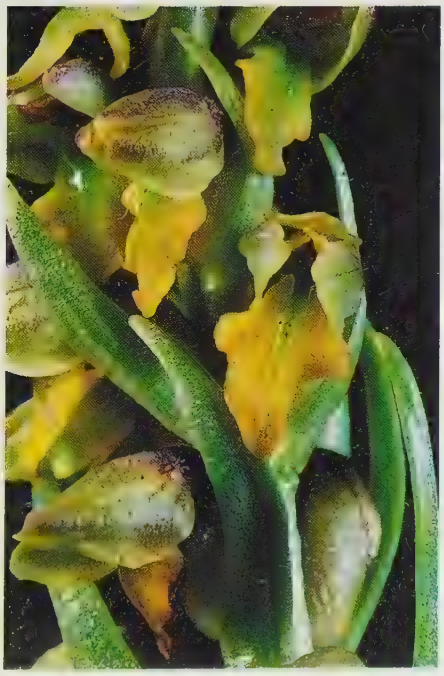


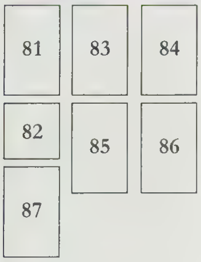




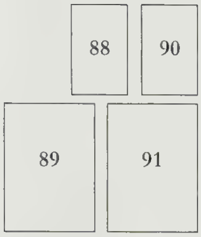








81 *Barlia robertiana*, United Kingdom (Photo: P. Cribb)
82 *Bartholina burmanniana*, South Africa (Photo: F. Duckitt)
83 *Benthamia praecox*, Madagascar (Photo: J. Hermans)
84 *Bonatea steudneri*, Malawi (Photo: P. Cribb)
85 *Brachycorythis pleistophylla*, Malawi (Photo: P. Cribb)
86 *Centrostigma occultans*, Malawi (Photo: P. Cribb)
87 *Chamorchis alpina*, Italy (Photo: P. H. Davies)

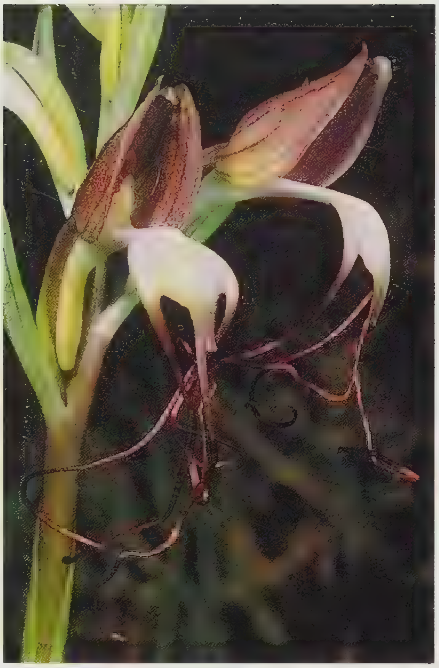


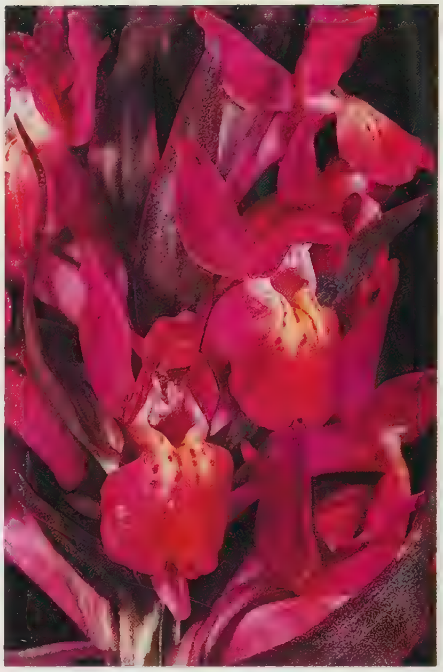
88 *Comperia comperiana*, Turkey
(Photo: P. H. Davies)

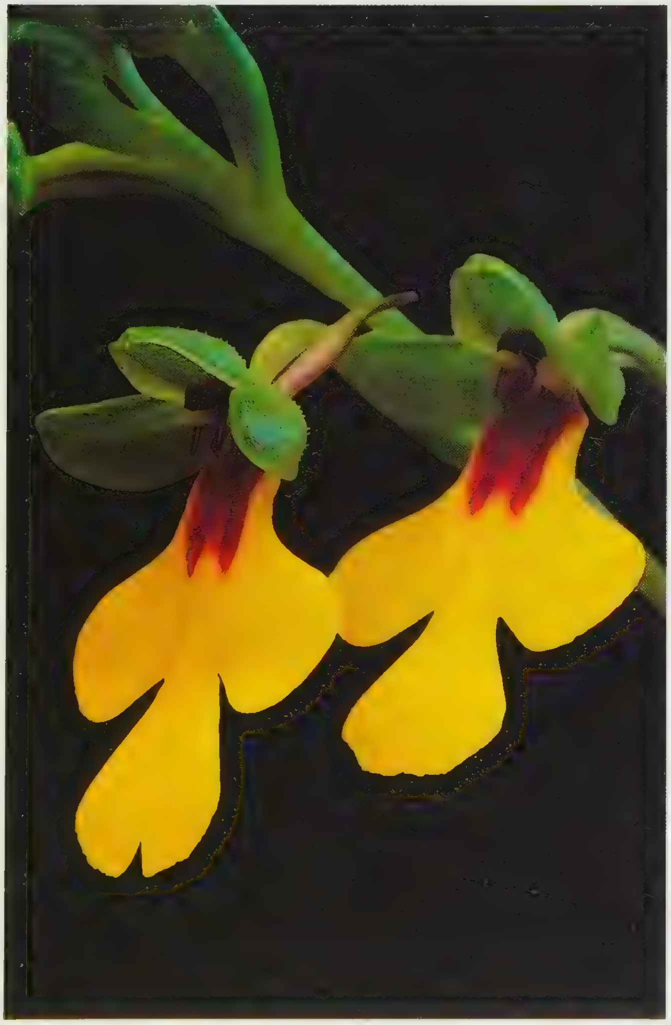
89 *Cynorkis flexuosa*, Madagascar
(Photo: J. Hermans)

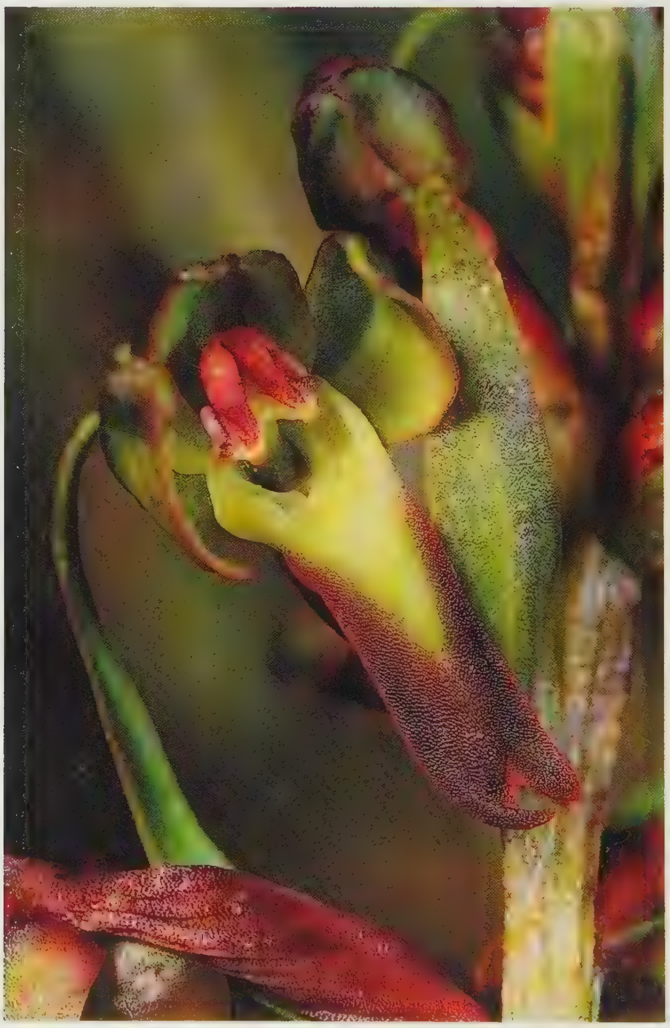
90 *Dactylorhiza sambucina*, France
(Photo: P. H. Davies)

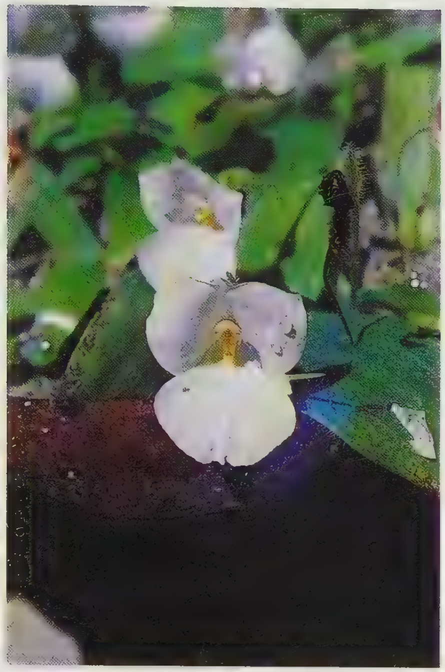
91 *Dactylorhiza viridis*, United Kingdom
(Photo: P. H. Davies)

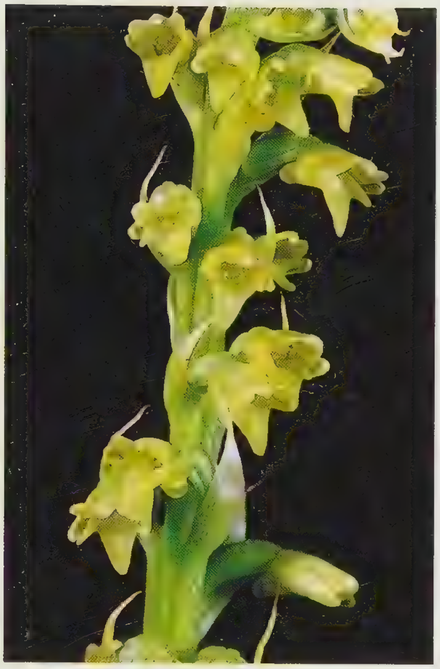


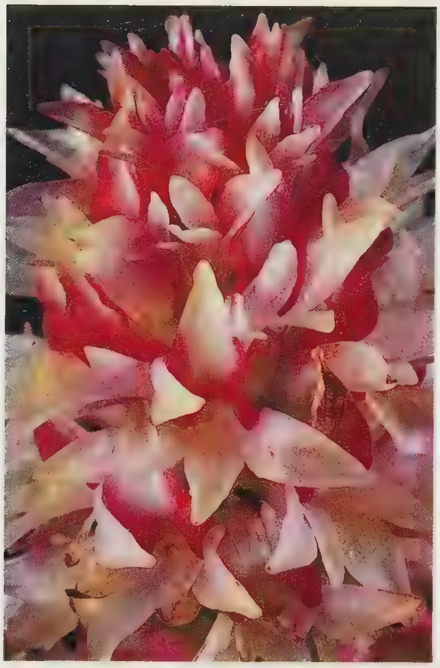


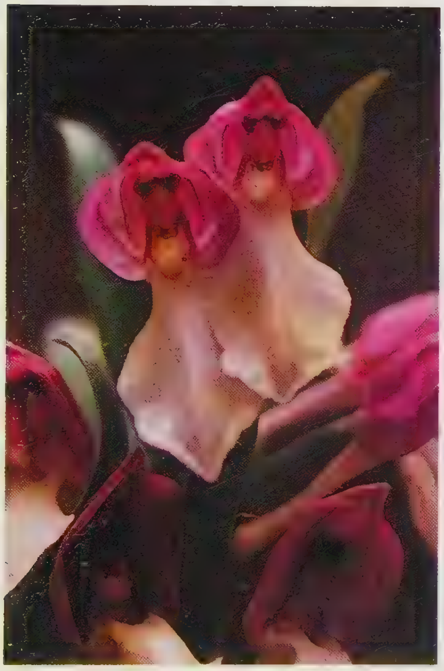


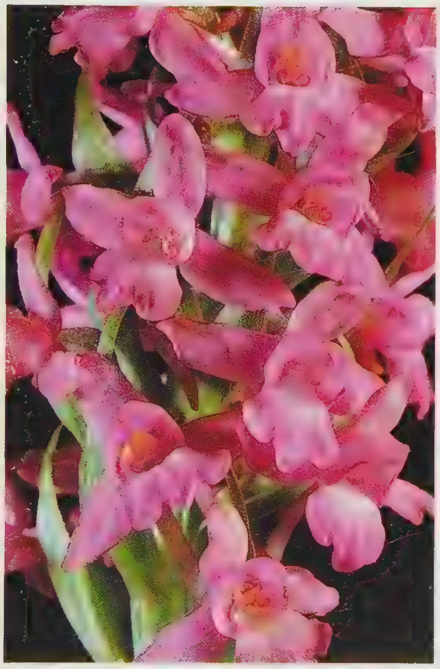


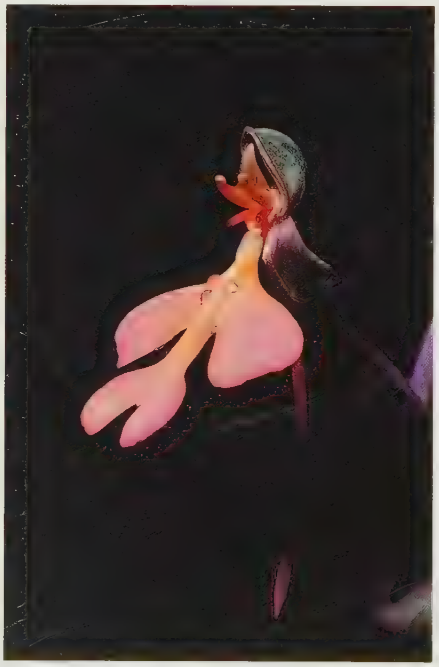






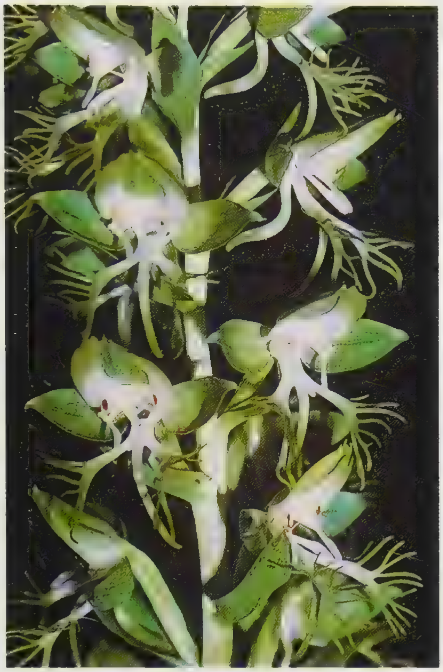


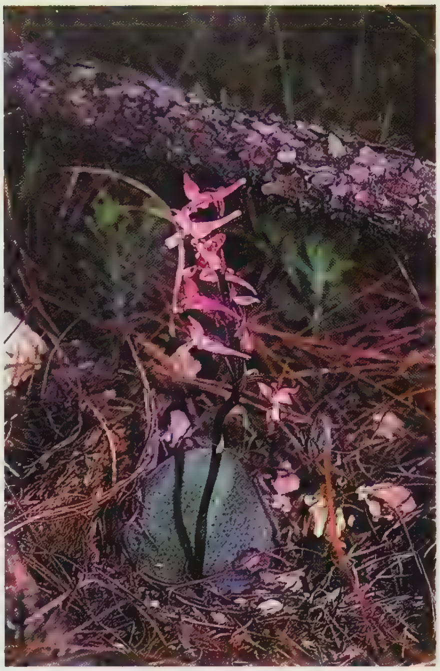


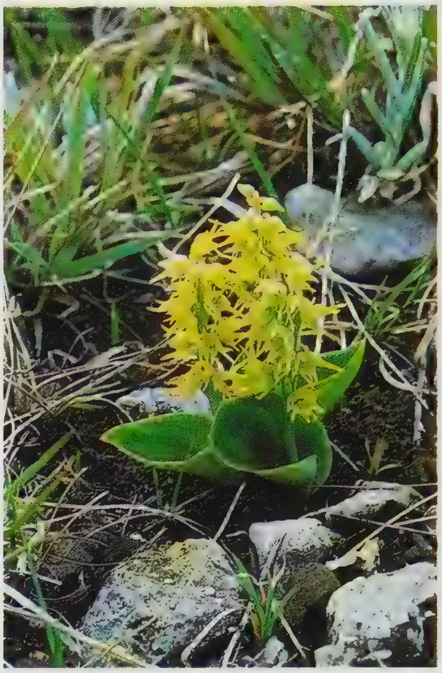


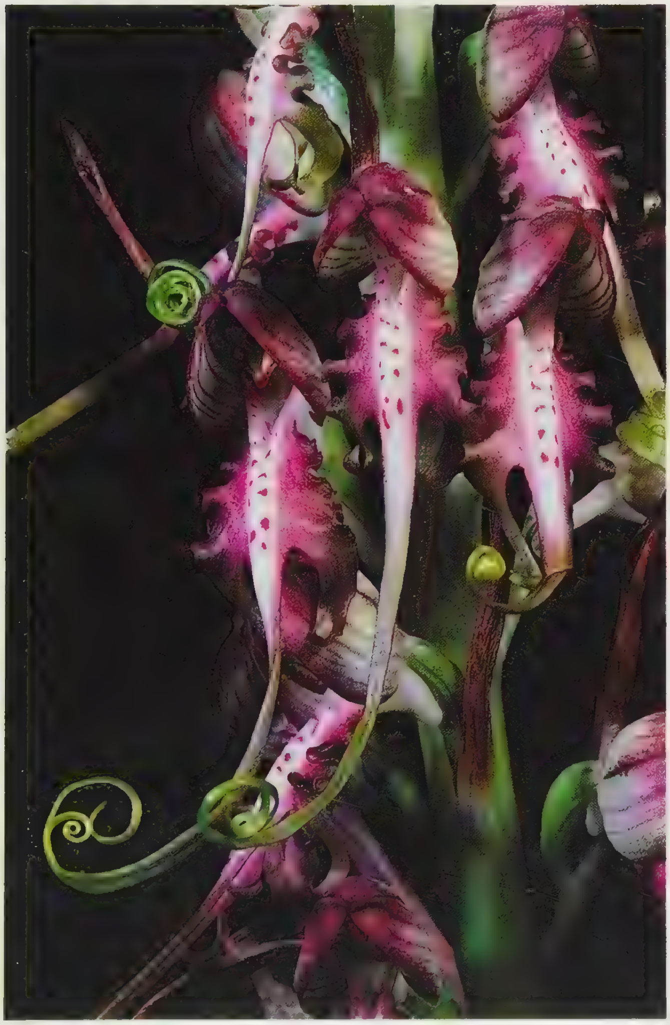
92	94	96
93	95	97

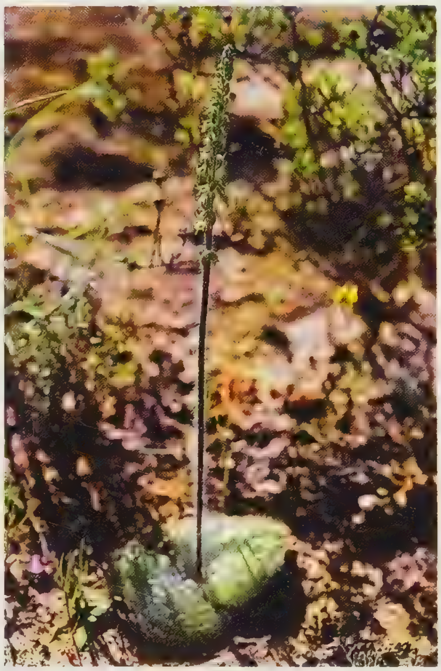
92 *Diplomeris hirsuta*, cultivated, India (Photo: U. Pradhan)
93 *Galearis spectabilis*, USA (Photo: S. Heilman)
94 *Gennaria diphylla*, Spain (Photo: P. H. Davies)
95 *Gymnadenia densiflora*, United Kingdom (Photo: P. H. Davies)
96 *Gymnadenia lithopolitanica*, Austria (Photo: P. H. Davies)
97 *Habenaria rhodocheila*, cultivated, USA (Photo: A. M. Pridgeon)

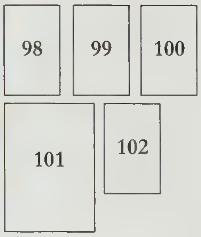












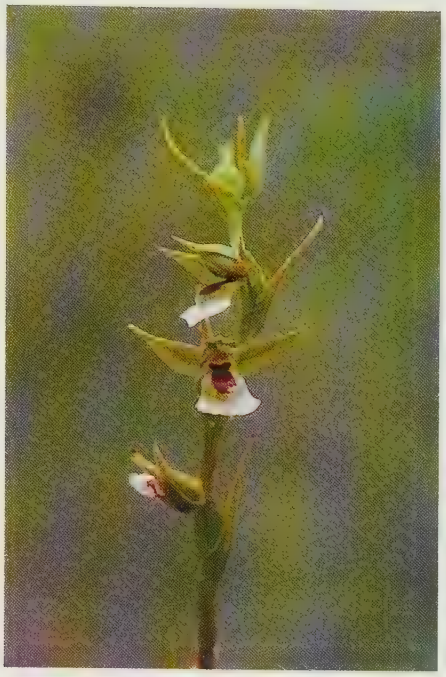
98 *Habenaria praestans*, cultivated, South Africa (Photo: A. M. Pridgeon)

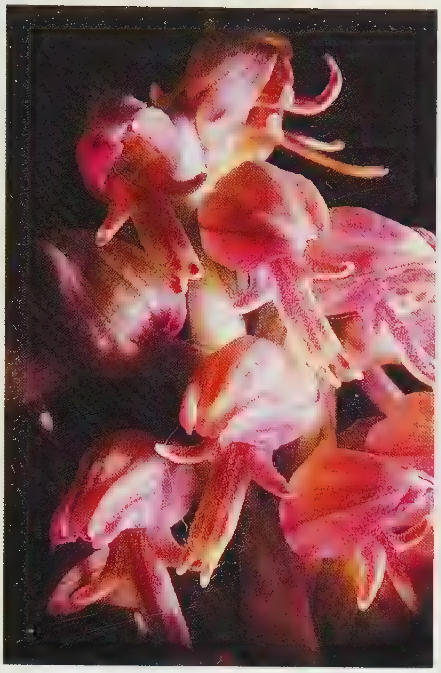
99 *Hemipilia cruciata*, China (Photo: P. Cribb)

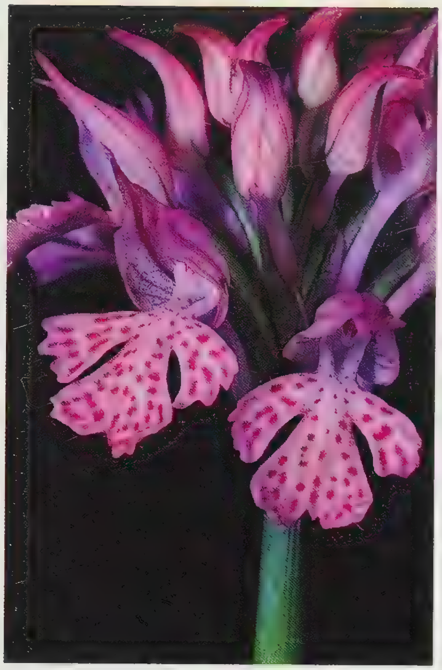
100 *Herminium ophioglossoides*, China (Photo: P. Cribb)

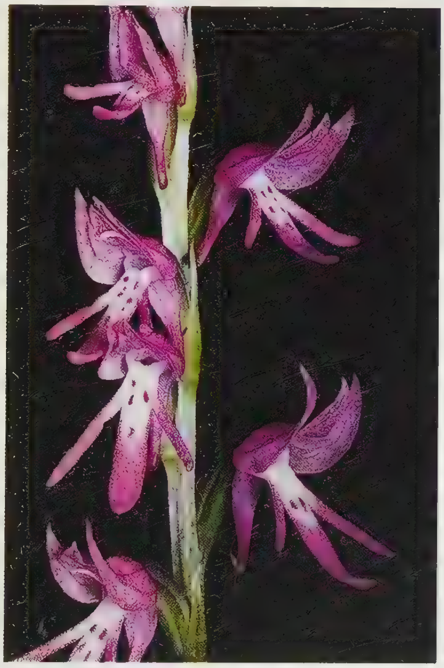
101 *Himantoglossum caprinum*, Turkey (Photo: P. H. Davies)

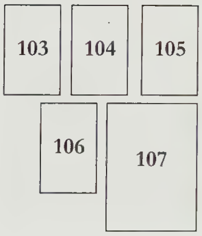
102 *Holothrix squamulosa*, Zaire (Photo: P. Cribb)

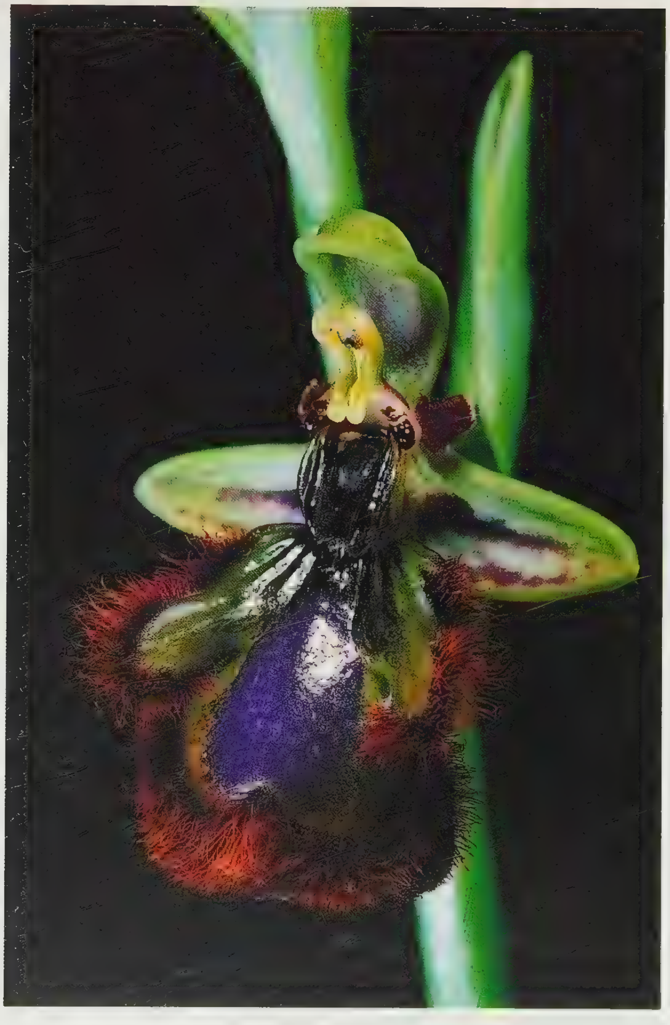




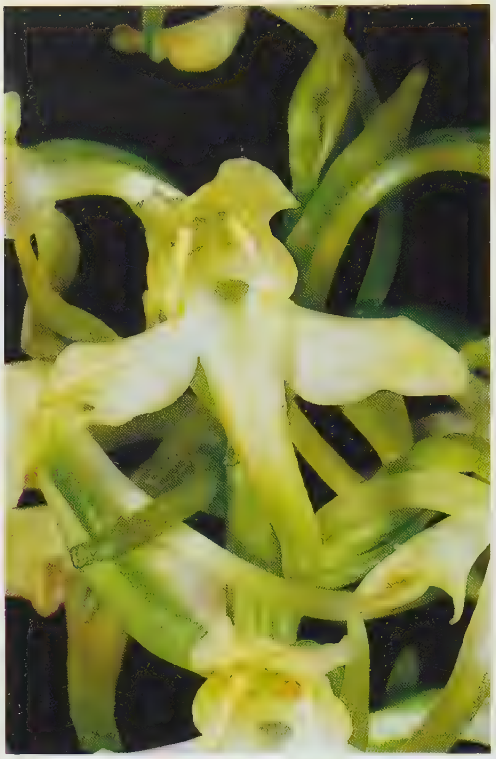


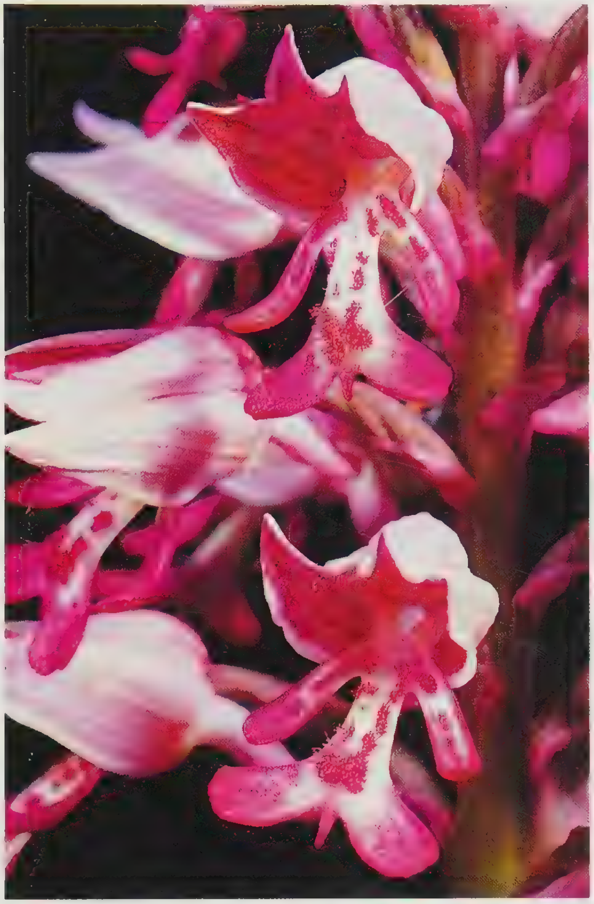


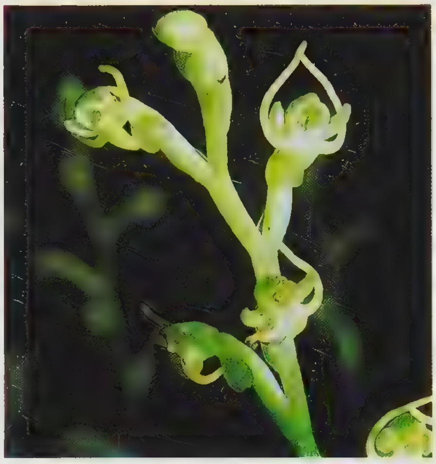


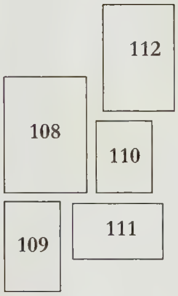


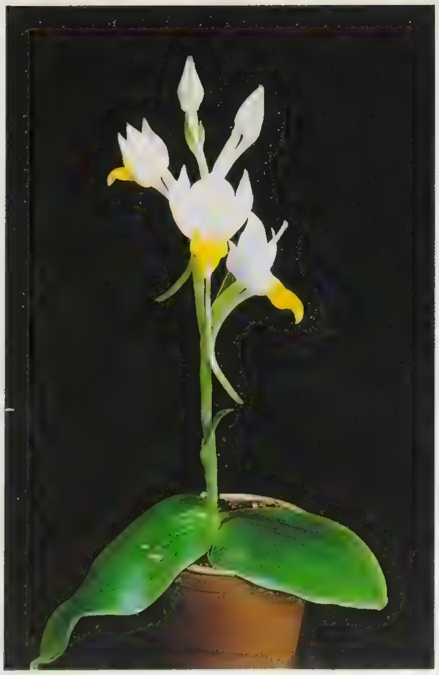
103 *Neobolusia stolzii*, Malawi (Photo: H. Kurzweil)
104 *Neotinea maculata*, Cyprus (Photo: P. H. Davies)
105 *Neotinea tridentata*, Greece (Photo: P. H. Davies)
106 *Neottianthe cucullata*, Turkey (Photo: C. A. J. Kreutz)
107 *Ophrys speculum*, Sicily (Photo: P. H. Davies)

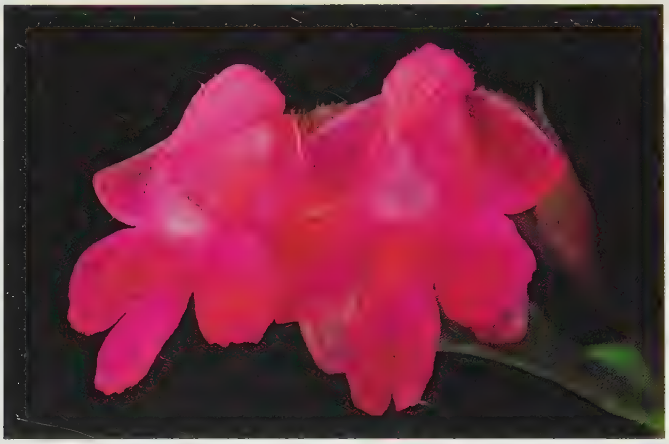












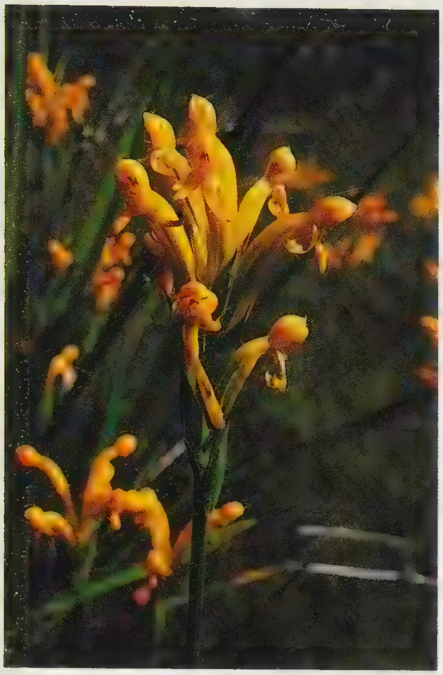
108 *Orchis militaris*, Germany
(Photo: P. H. Davies)

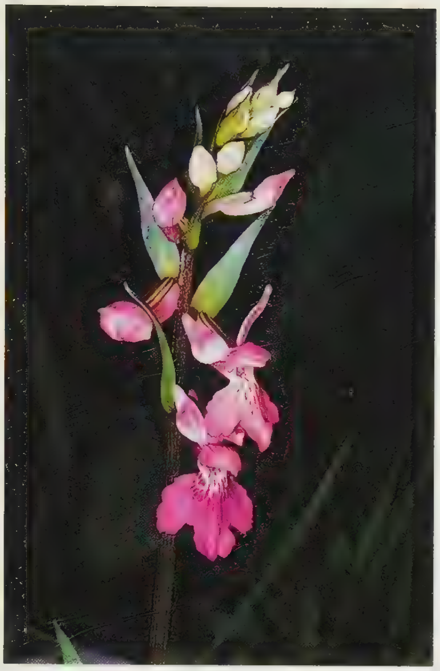
109 *Pecteilis sagarikii*, cultivated, Thailand
(Photo: Royal Botanic Gardens, Kew)

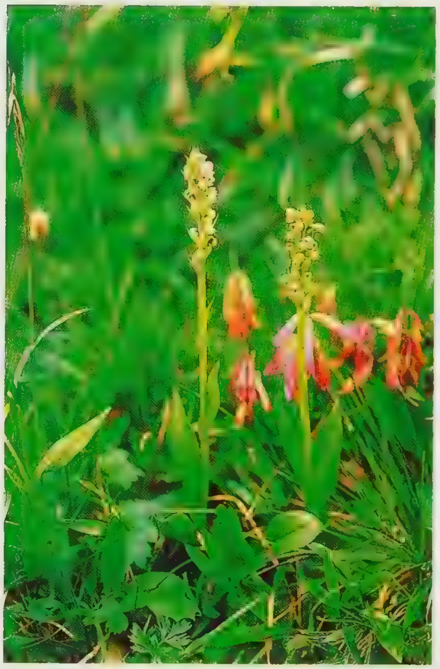
110 *Peristylus monticola*, Malaysia
(Photo: J. Dransfield)

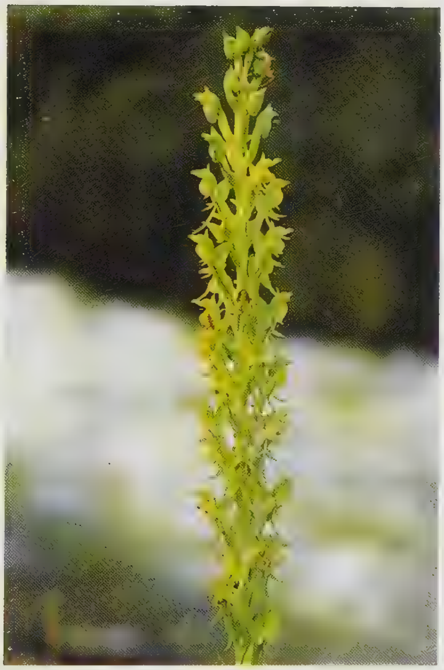
111 *Physoceras violaceum*, Madagascar
(Photo: J. Hermans)

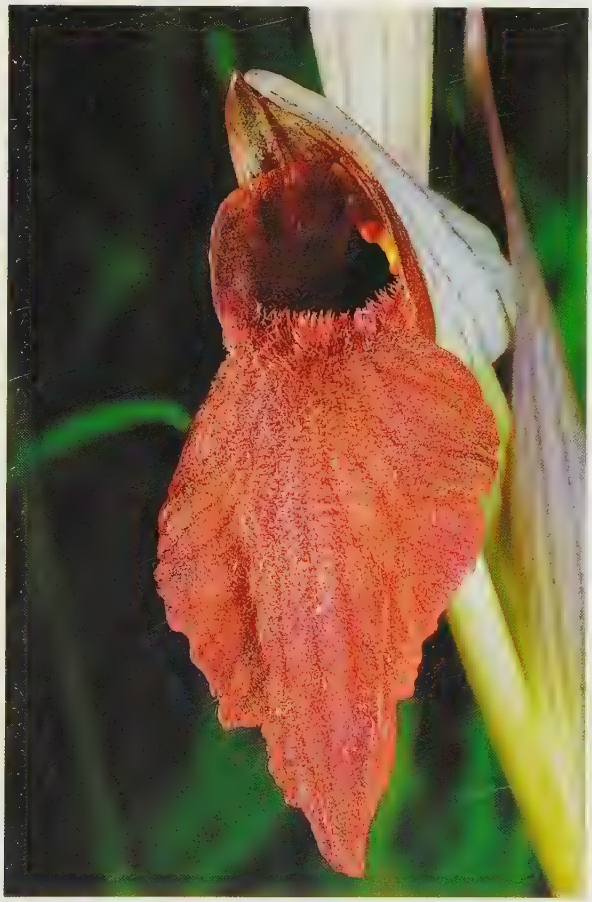
112 *Platanthera chlorantha*, United Kingdom
(Photo: P. H. Davies)

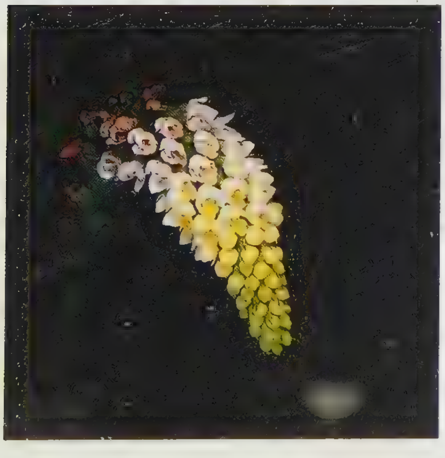


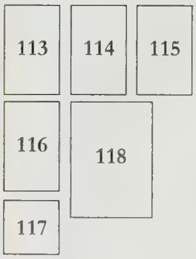












113 *Platycoryne buchananiana*, Malawi (Photo: P. Cribb)

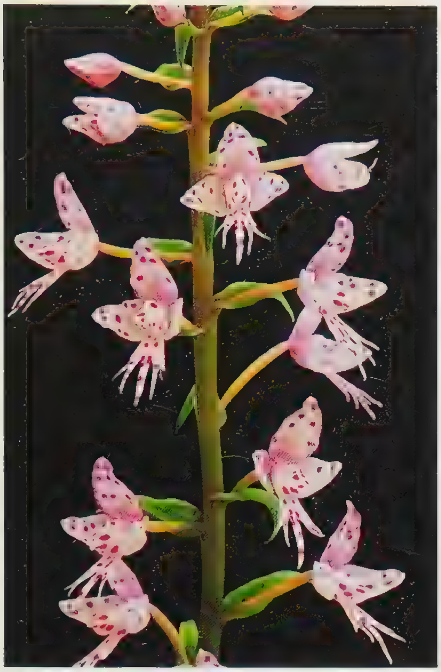
114 *Ponerorchis chusua*, China (Photo: P. Cribb)

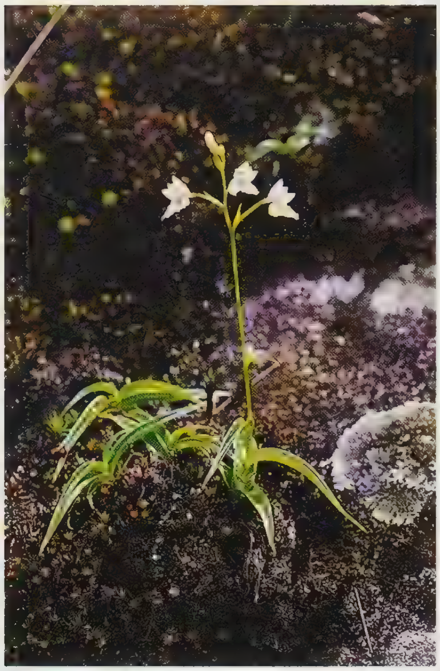
115 *Pseudorchis albida*, Switzerland (Photo: P. Cribb)

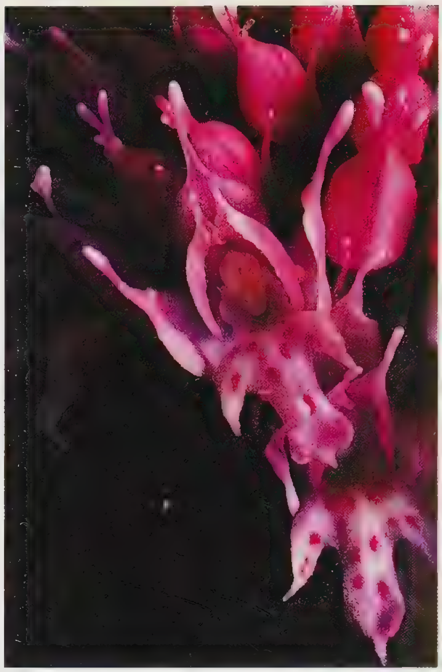
116 *Roeperocharis bennettiana*, Malawi (Photo: P. Cribb)

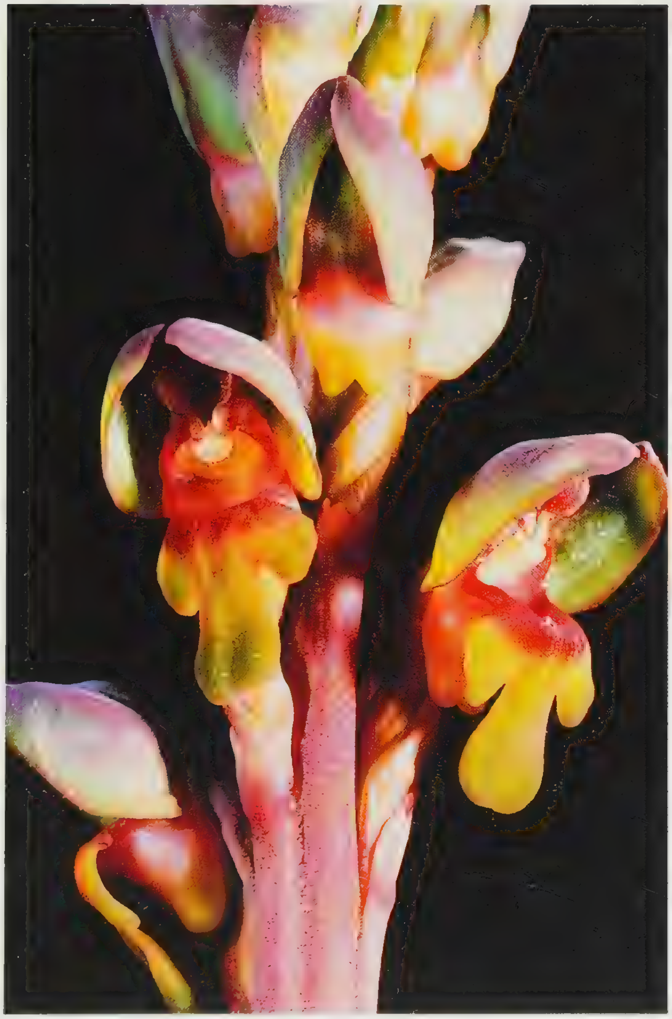
117 *Schizochilus cecilii*, Zimbabwe (Photo: P. Cribb)

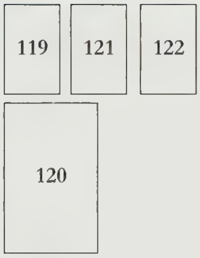
118 *Serapias cordigera*, Greece (Photo: P. H. Davies)











119 *Stenoglottis longifolia*, cultivated, United Kingdom
(Photo: J. Hermans)

120 *Steveniella satyrioides*, Turkey
(Photo: P. H. Davies)

121 *Thulinia albolutea*, Tanzania
(Photo: S. Manktelow)

122 *Traunsteinera globosa*, France
(Photo: P. H. Davies)

response to drought, occur in a number of species of Disinae, Coryciinae, and Brownleeinae (Chesselet 1989). Some cells contain starch grains, raphide bundles, and very rarely tannins. Vascular bundles generally collateral and arranged in one series across the leaf, commonly attached by parenchymatous tissue to either the upper or lower epidermis, and only few of the bundles are entirely free in the mesophyll. Sclerenchyma bundle caps occur in all studied species of *Disa* sections *Stenocarpa* and *Herschelianthe*, and occasionally in *Ceratandra* and *Disa* sections *Emarginatae*, *Repandra*, and *Amphigena*. (**HK, PL**)

Stem

AERIAL STEM

Hairs absent (except in *Disa glandulosa* and a few *Disperis* species). Cuticle thin (1–4 μm). Epidermis uniseriate. Cortex comprises thin-walled cells containing starch grains and bundles of raphides. Although the cortex is usually compact, its cells sometimes degenerate, resulting in lacunae (some *Disperis* and *Schizodium* species). Sclerenchymatous ring of 3–8 cell layers between cortex and ground tissue. Ground tissue consists of parenchymatous cells around the vascular bundles and in the centre of the stem. In old stems the ground tissue frequently degenerates, forming a columnar lacuna. Vascular bundles collateral, occasionally with parenchyma or sclerenchyma caps, rarely developed as bundle sheaths. Most vascular bundles occur in ground tissue, but a few are also present in the cortex. Vascular bundles of the ground tissue arranged in 1–5 rings, the number of rings and bundles depending on stem diameter. Sclerenchyma caps are particularly well developed in several *Satyrium* species, although their occurrence is subject to slight variation within the same species.

UNDERGROUND STEM

The portion of the stem just above the tuber, corresponding to the dropper of the previous season, is often well developed. Structure similar to that of aerial stems except that vascular tissue is concentrated centrally. Underground stems frequently enclosed by a sheath, derived from the dropper of the previous season. The sheath can be used as a 'growing canal' more than once: dropper and underground stem may alternately grow through the same sheath, a phenomenon that also occurs in the underground organ of *Ceratandra* (see below) and many Diurideae.

Tuber

Root tubers are generally present in Diseae. The two species of *Disa* sect. *Stoloniferae* lack tubers (Linder 1981*c*). Tubers are sometimes also said to be absent in *Ceratandra*, but occasionally specimens with small but clearly visible tubers have been collected. Velamen 1–3 layered. Cortex: cells large, normally thin-walled, with comparatively large aggregations of glucomannoglycans (Mabusela *et al.* 1989). Two types of vasculature occur in the tribe: 1) in most species the siphonostele is not dissected and comprises a ring of alternating xylem and phloem elements; and 2) the siphonostele is dissected into 5–25 meristeles in all 21 examined *Satyrium* species, *Disa* sections *Amphigena*, *Stenocarpa*, *Herschelianthe*, and two *Disperis* species. Each meristele has a one-layered endodermis and pericycle.

An unusual underground organ is found in *Ceratandra* sect. *Ceratandra*, consisting of a complex fascicle of roots and an underground stem, all of which are surrounded by a hairy sheath. The cortices of stem and roots are strongly angular-collenchymatous. At the end of the season the entire complex dies, and it is assumed that the new shoots grow through the dead fascicle. Underground stolons with a stem structure also occur in *Disa tripetaloides* (L.f.) N.E. Br., *D. cardinalis* H. P. Linder, and *D. uniflora* Bergius.

Dropper/root-like stolons

Young tubers are frequently developed directly on the stem base and are therefore sessile. However, in a number of species they are positioned on elongate stalks called droppers. These are usually up to 40 mm long (rarely up to 90 mm) and have the structure of a root. The stele may be dissected or not. In a few species there are also root-like stolons with developing tubers at the apex (*Satyrium odorum* Sond., *S. ligulatum* Lindl., *Corycium orobanchoides* Sw., *C. excisum* Lindl., *Pterygodium schelpei* H. P. Linder).

Root

Roots of Diseae are generally few in number, usually fairly thick (1–3 mm), and normally arise at the base of the stem just above the tuber. Hairs unicellular and sparse. Velamen uniseriate (rarely 2–3 layers); outer cell walls usually convex. Cortex, bounded by a clearly developed exodermis and endodermis, massive, containing collapsed cells with fungal pelotons and raphide bundles. The stele is surrounded by a one-layered pericycle with alternating xylem and phloem elements around a central parenchymatous pith. (**HK, PL**)

Palynology

A palynological survey of Diseae was undertaken by Chesselet and Linder (1993). Eight species were studied by means of TEM and 85 by SEM. Most of the species belong to subtribes Disinae, Huttonaeinae, Brownleeinae, and Coryciinae. The pollinium surface ornamentation of a large number of Satyriinae was examined by Kurzweil and Linder (1999). Pollen ornamentation data of a number of *Disperis* species are given in Manning and Linder (1992). Pollen massulae are rounded to elongate in all Diseae except in Coryciinae excluding species of *Disperis* (= Coryciinae *s.s.*), which have fasciculate massulae. Tetrads are usually isodiametric, but elongate tetrads occur in *Huttonaea* and Coryciinae *s.s.* and may indicate a close relationship.

As seen in transections, the pollen of Diseae varies from semi-tectate to tectate. It was suggested that the semi-tectate exine as observed in Satyriinae, Disinae, and *Disperis* is primitive in Diseae (Chesselet and Linder 1993).

Characters of the pollen ornamentation do not distinguish the species but are informative at the generic and subtribal levels. A reticulate pattern may be primitive with respect to Diseae (Chesselet and Linder 1993). Satyriinae mostly have a variously hamulate ornamentation, although a reticulate or 'crisp-reticulate' pattern is found in several species of the *Satyrium odorum* Sond.-*parviflorum* Sond. group (Kurzweil and Linder 1999). *Disa* (Disinae) is characterized by a rugose or verrucose exine, and the examined species of *Schizodium* (Disinae) have a broken-reticulate pattern (Chesselet and Linder 1993). Pollen characters provide three synapomorphies for Coryciinae *s.s.*, namely fasciculate massulae, elongate tetrads, and a secondarily tectate exine. The exine of *Disperis* (Coryciinae) is either reticulate or baculate (Manning and Linder 1992; Chesselet and Linder 1993). In *Brownleea* (Brownleeinae) the exine pattern is reticulate (Chesselet and Linder 1993). **(HK, PL)**

Phytochemistry

Phytochemical studies in Diseae are limited to a single report that describes the detection of flavone *C*-glycosides in *Disa uniflora* Berg. (C. A. Williams 1979). **(NV, RG)**

Phylogenetics

Diseae have long been regarded as a monophyletic group based on a reflexed anther orientation. However, reflexed anthers also occur occasionally in Orchideae (for example slightly reflexed in *Draco-monticola*, horizontal in *Habenaria* sect. *Kryptostoma*), and several Diseae have erect or suberect anthers (*Huttonaea*, *Disa* sect. *Micranthae*, *Pterygodium* sect. *Ommatodium*). This indicates that the anther orientation may not be a uniquely derived character.

Moreover, extensive research into Diseae over the last few decades has not yielded any additional characters that could serve as synapomorphies for the tribe and would therefore support its monophyly. Diseae are closely related to the Orchideae. Linder (1986*a*) suggested that the usually spurred and complex lip of Orchideae could act as synapomorphy for that tribe, since Diseae generally have simple lips.

Recent molecular results do not support the monophyly of Diseae and instead indicate that Orchideae are embedded in the Diseae and that Diseae are therefore paraphyletic. Sequence data from the plastid gene *rbcL* indicate that *Disa* is sister to Diseae plus Orchideae, and that *Satyrium* is sister not to *Disa* but to a paraphyletic Habenariinae (Cameron *et al.* 1999). However, internal support for this arrangement is weak, and Kores *et al.* (1997) with the same data obtained other, equally parsimonious arrangements that are congruent with a monophyletic Diseae, sister to a monophyletic Orchideae. However, only two species of Diseae and four of Orchideae were sampled for *rbcL*, and these results could be due to undersampling. A detailed analysis of Diseae based on the ITS sequences of nuclear ribosomal DNA (Douzery *et al.* 1999) found strong evidence for the paraphyly of Diseae, with the specialized genus *Disperis* sister to all other ingroup taxa, followed by Disinae, Coryciinae *s.s.*, Satyriinae, and finally Orchideae. For this treatment we will still follow the 'old' classification, but it is clear now that plastid DNA sequences also indicate that Diseae are paraphyletic (Kores, Molvray, Chase, *et al.*, unpublished).

Five subtribes are currently recognized: Satyriinae, Disinae, Huttonaeinae, Brownleeinae, and Coryciinae (Linder and Kurzweil 1994; Kurzweil *et al.* 1995; Linder and Kurzweil 1999). Of these, Satyriinae, Disinae, and Coryciinae were also recognized in the past (e.g. Dressler 1981, 1993), and Huttonaeinae and Brownleeinae were added following the phylogenetic analysis of Linder and Kurzweil (1994). Huttonaeinae, with *Huttonaea* as its sole genus, has previously been placed in tribe Orchideae (Dressler 1981) but was transferred to Diseae on the basis of morphological (Kurzweil 1989) as well as pollen characters (Chesselet and Linder 1993). The genus shows affinities to Coryciinae. Brownleeinae, with *Brownleea* as its sole genus, shares several characters with both Disinae and Coryciinae, and as a consequence Linder and Kurzweil (1994) suggested that the genus may be of hybrid origin. Both *Huttonaea* and *Brownleea* are atypical in their flower structure, and it was considered taxonomically most informative to place both genera in monogeneric subtribes (Linder and Kurzweil 1994).

Cladistic analysis of the variation in the nucleotide sequences of the nuclear ITS (Douzery *et al.* 1999) is congruent with recognizing the Satyriinae, Disinae, and Brownleeinae. However, Coryciinae are polyphyletic, as *Disperis* is not included with *Corycium* and *Pterygodium* as members of the Coryciinae *s.s.* However, the sampling was not as thorough as it might have been. In Disinae, the ancestral subclade is probably *Schizodium*; in Satyriinae it is *Pachites* (Kurzweil and Linder 1999), and in Coryciinae it comprises *Ceratandra* and *Evotella*. If there were any mistakes in the Linder and Kurzweil classification of the tribe, these are the genera most likely to be misplaced. On the whole, the molecular data are largely consistent with the subtribes recognized on morphological data, with the exception of Coryciinae.

We follow a conservative approach to the generic delimitations, recognizing a smaller number of broad genera, rather than a large number of narrowly delimited genera. The current genera were mostly delimited by Swartz in 1800. Lindley (1830–1840) divided up these large genera, splitting off as many segregates as he could maintain. Schlechter recombined these into a small number of large genera (Schlechter 1898, 1901). His generic taxonomy is similar to the taxonomy followed here. Scarcely a decade later Rolfe (1912–1913) resurrected most of Lindley's genera, and added more to them by consistently recognizing flower resupination (or the lack thereof) as a 'generic' character. The history of the post-Rolfean orchid taxonomy is one of synonymizing his genera, so that now we have reached a situation reminiscent of the taxonomy advocated by Swartz and Schlechter. **(HK, PL)**

Uses

Economic uses of species of Diseae are mainly confined to horticulture (Wodrich 1997), and other uses are minor. Among the species frequently found in cultivation are *Disa uniflora* and related species with large flowers and striking colours. Although not easy to grow, these orchids are particularly common in collections in the

Western Cape of South Africa. However, the species are also grown in overseas nurseries, botanical gardens, and private collections. The species is also extensively used in hybridization programs (Vogelpoel 1992). Other species of Diseae are seldom found in living collections, as most of them have small flowers with little appeal to collectors.

In several species of Diseae the tubers are used as source of food for local communities in parts of tropical Africa (Lawler 1984; Geerinck 1984; G. Williamson, personal communication; notes on herbarium sheets in K). However, there is no evidence of harvesting them on a large scale, and it can be assumed that the relevant species are collected in the wild. Obviously only species with large tubers can be used (certain *Satyrium* and *Disa* species). In the past a sweet juice was made from tubers and roots of *Disa barbata* Sw., *D. venusta* Bolus, *Satyrium bicorne* (L.) Thunb., *S. candidum* Lindl., *S. carneum* (Dryand.) Sims, and *S. erectum* Sw. (Lawler 1984). Parts of a few species of Diseae seem to have medicinal properties (*Satyrium bracteatum* Thunb., *S. nepalense* D. Don, *Disa chrysostachya* Sw., *D. polygonoides* Lindl., and *Ceratandra grandiflora* Lindl.; Rayner 1977; Lawler 1984). *Disa chrysostachya* was previously used to make a human poison (Rayner 1977), and a fish poison was made from tubers of *Satyrium amblyosaccos* Schltr. (Geerinck 1984).

Various species of Diseae also play a role in superstition in rural areas of Africa. In South Africa several orchids are collected on a large scale for this purpose and sold to local '*muthi*' markets, which caused major concern as it may threaten certain orchid populations (McDonald and Duckworth 1994). A tea or body wash with parts of *Corycium nigrescens* Sond., *Disa stachyoides* Rchb.f., and *D. versicolor* Rchb.f. is believed to repel evil (Rayner 1977; Lawler 1984; McDonald and Duckworth 1994). *Satyrium parviflorum* Sw. is sometimes used as a love charm (Rayner 1977; Lawler 1984; McDonald and Duckworth 1994). A fertility charm is made from *Corycium nigrescens* and *Disa aconitoides* Sond. (Rayner 1977; Lawler 1984; McDonald and Duckworth 1994). The use of *Disa stachyoides* is common in rural parts of southern Africa as it is believed that the orchid repels lightning (McDonald and Duckworth 1994). **(HK, PL)**

Cultivation

Growing South African terrestrial orchids is complex as the species come from widely differing habitats. Since nursery-raised plants are becoming available, it is essential to understand the differing cultural requirements when planning to grow a particular species. The following basic principles should serve as a guide.

Twelve climatic regions have been defined, determined largely by the rainfall pattern and topography (Wodrich 1997). It is essential to know the rainfall pattern of the habitat. This may be winter rainfall, summer drought, summer rainfall, winter drought, or a year-round rainfall with a tendency to summer dormancy. Furthermore, there are marked differences in the habitat which can be conveniently classified into Cape fynbos, grassland, either dry or moist, wetlands, forest margin, woodlands, and mountain cliffs.

The majority of the terrestrial orchids are deciduous due to long periods of drought-inducing dormancy. However, there are a few species of *Disa* that are associated with perennial mountain streams, require no dormancy, and are designated evergreen. The two groups need to be separated because of their widely different cultural management.

Deciduous species

When and when not to water is the single most important requirement because most plants are lost by an unforgiving and irreversible rot if water is given during the dormant period. For this reason, plants from the winter rainfall region are best kept entirely separate from those from the summer rainfall area, whereas those from the year-round rainfall region are kept dry during dormancy and watered when dormancy is broken.

How can one tell when to water? This is easy when the pots are kept separate. Generally, plants from the winter rainfall area will have been kept cool and dry in their containers usually from October/November (late spring) throughout the hot summer months until April/May (autumn) when the emergence of leaves signals regrowth. Plants showing this activity can be moved to a suitable sheltered area under a transparent roof and given more light. Water is then provided very sparingly for a few weeks because roots emerge and grow very slowly from the stem above the tuber. Once the leaves are growing rapidly, liberal watering should be commenced.

Conversely, plants from the summer rainfall area are kept dry and cool in their containers from March/April to September/October when dormancy is broken with the arrival of summer rains. Although these rules work well for most of the well-known species from the different rainfall areas, there are many desirable species that have proved intractable. This applies particularly to the species which are confined to marshes, bogs, and wetlands.

Our personal experience has been limited to relatively few species but with more seed-raised plants becoming available, good progress is anticipated. *Disa sagittalis* Sw. and *Brownleea coerulea* Harv. ex Lindl., both from the year-round to summer rainfall areas, are easy. *Satyrium coriifolium* Sw., *S. carneum* R. Br., *S. odorum*, and others from the winter rainfall area are amenable and rewarding (Wodrich 1998). Highly desirable but more difficult are *Disa lugens* Bolus, *D. purpurascens* Bolus, *D. spathulata* Sw., as well as *D. cornuta* (L.) Sw.; *Disa longicornu* L.f., and *D. maculata* L.f. are even more fastidious, demanding simulation of their cliff-face habitats.

Growing medium and containers

Size of the pots depends on the size of the tubers. Extra holes are made to improve drainage. The potting mix should combine river sand and grit to permit good drainage, and good quality loam with fine bark chips helps to retain moisture and add nutrients. Leaf-derived compost supplies trace elements, and a top dressing of well-composted pine needles from pine forests is a possible source of mycorrhiza. The addition of fine sand, benefiting some taxa such as *Satyrium* and *D. lugens*, can greatly prolong drying out between waterings when plastic pots are used. Clay pots ensure more efficient drying out of the sand and are therefore preferred for these species. Crock and pebbles are always used below to ensure efficient bottom drainage.

Temperature

This ranges from 5–10°C in winter to 20–30°C in summer.

Light

Light is increased to ensure optimal photosynthesis within the developing leaves. Once mature, the plants benefit from full exposure to sunlight for part of the day. However, species of the forest margin and forest floor prefer semi-shade.

Water

Pure water, low in salts, is essential to avoid harmful build-up of salts in the medium. Watering commences sparingly once the new growth emerges but should be increased as the plant matures and new roots have formed. Allow pots to dry out between waterings, and never allow water to collect in leaf axils or 'cups' or at the developing point of the tubers, which could cause bacterial or fungal rot. Abundant air movement and watering only in the early morning helps keep the leaves dry. Mature plants can be given a thorough watering once a week, but from the moment the leaves turn yellow water should be completely withheld to prevent stem rot extending into the tuber.

Feeding

Fertilizers are best avoided or else used diluted because all the nutrition required by the plant is derived from the compost and mycorrhiza.

Repotting

The best time for repotting is when the tubers are fully dormant in a completely dry medium. At this stage the tubers can either be repotted into fresh medium or kept in dry wood shavings in a paper bag and kept cool and dry until sprouting commences. Success depends on meticulous management, labelling, and following the well-defined periods of growth and dormancy.

Evergreen species

There are seven species in this group, of which three have been well known for over 100 years: *D. uniflora*, *D. tripetaloides* N.E.Br., *D. aurata* (Bolus) L.T.Parker & H.Koopowitz, *D. cardinalis* H.P.Linder, *D. racemosa* L.f., *D. venosa* Sw., and *D. caulescens* Lindl. They all come from the Western Cape, a winter rainfall area, but *D. tripetaloides* is also found in Natal. Two species, *D. racemosa* and *D. venosa*, differ in having a seepage marsh habitat and a fire-dependent flowering.

The cultural requirements of the evergreen group are so different from the deciduous group that they should be grown in a separate area. Success depends on understanding the natural habitat and how the plants adapt to the marked seasonal changes in the Western and South Western Cape (Vogelpoel 1993). Throughout the dry summer months, water in the mountain streams is sustained by the frequent cloud-bearing southerly winds.

Water

Water must be constantly provided, though less in winter, to ensure that the growing medium never dries out. Water may be delivered to the pots from above or below, using a tank for hydrocultural or ebb-and-flow irrigation. Water quality is of crucial importance. The pH should be 5.0–6.0, and the salt content below 200 ppm. Rainwater is ideal. Hard water is unsuitable unless the salts are removed by reverse osmosis or de-ionizing techniques.

Growing medium and containers

Various media have been used with success in different parts of the world. The most popular are dead sphagnum moss (with or without live sphagnum as a surface cover), silica or washed river sand, pumice pebbles, Styrofoam, and peat. In principle, the medium should be well drained and aerated and contain some form of compost (peat, pine bark compost, palm fibre, or fern fibre) in the proportion 10 parts sand or pumice to 1–3 parts compost. With overhead watering use fine silica sand for better water-retention. A coarser mix is necessary for hydrocultural irrigation. Small (10–15 cm) pots, preferably deeper than wide with extra drainage holes, are best.

Temperature

The pot should be kept cool (winter 5–15°C, summer 10–23°C). High ambient temperature, up to 30°C, is acceptable in summer, as long as: there is adequate air movement; a suitable top dressing of either living sphagnum, coarse pebbles, or fern fibre is added to the growing medium; and watering is increased.

Humidity and air movement

Humidity should be above 60% with free air movement. Hot, dry winds are harmful.

Light

Bright, filtered sunlight assures optimal growth and colour potential in the growing season from spring to summer. Seedlings and young plants require more shade.

Feeding

Inorganic fertilizers containing macro and micro elements in weak concentration (less than 300 micro-Siemens) can be given safely as a plant and foliar feed several times a week during the active growth season from spring to summer. Salt build-up can be avoided by flushing with pure water between feedings. Fertilizing is withheld after flowering but resumed once the new tuber and growth appears four weeks or so after the old stem has begun to die. Feeding is then resumed and continued until the cold winter months, when both watering and feeding are drastically reduced to prevent fungal and bacterial infections.

Repotting

Repotting is best deferred until autumn when the new growths are vigorous. This allows time for the old plant to die and also for optimal development of the new tuber and other underground organs. Repotting at the correct time is highly beneficial.

Growing area

Evergreen disas should be grown in a special area and constantly observed throughout the seasons, while maintaining a high standard of hygiene and cleanliness to minimize fungal and bacterial rots. Pests such as thrips, mites, gall midge larvae, snails, slugs, and caterpillars should be eliminated by appropriate measures to prevent proliferation of pests and infected tissues.

Propagation

Plants may be propagated by division, seed, or tissue culture. The seed of the evergreen disas is large, adapted to water-borne distribution and spontaneous germination without mycorrhiza on a damp surface of peat or dead sphagnum (Kurzweil 1993). Asymbiotic *in vitro* germination is the preferred method; not only is maturation of seed as short as 6–8 weeks, but growth is so rapid that deflasking can be commenced after only one year. Thus flowering-size plants can be produced 2–3 years after pollination. **(LV, SC)**

SUBTRIBE BROWNLEEINAE

Brownleeinae H.P.Linder & Kurzweil, *Ann. Mo. Bot. Gard.*, **81**, 710 (1994). Type: *Brownleea* Harv. ex Lindl.

Description

Glabrous terrestrial *herbs* with root tubers. *Leaves* cauline. *Dorsal sepal* hood-like and spurred as in Disinae. *Petals* united with the dorsal sepal like in Coryciinae. *Labellum* a minute linear organ, shorter than the column and basally fused with it. *Column* without prominent stalk; anther reflexed with knee-like angled thecae; pollinia two, sectile; stigma a slightly convex pad on the front side of the column; rostellum mostly two-lobed. **(HK, PL)**

8. BROWNLEEA

Brownleea Harv. ex Lindl., *J. Bot.* (*Hooker*), **1**, 16 (1842). Type species: *Brownleea parviflora* Lindl. (lecto.).

Derivation of name

After Rev. John Brownlee (1791–1871), a Scottish missionary and gardener, who was living in what is now called Kingwilliamstown (eastern Cape Province of South Africa) and sent plant specimens to William Henry Harvey. **(HK, PL)**

Description (Plate 1; Fig. 8.1)

Slender terrestrial or occasionally epiphytic *herbs* with pubescent to woolly tubers, glabrous in all above-ground parts. *Stem* with brown sheathing leaf above the tuber. *Foliage leaves* one to few, cauline, ovate to linear. *Inflorescence* terminal, dense head-like cluster or lax to dense raceme, rarely flowers solitary; bracts shorter to longer than the ovary, acuminate, green, erect. *Flower* white, pink or mauve, often darker-spotted. *Dorsal sepal* galeate and spurred, adnate to the petals, acute; spur cylindrical or clavate, horizontal at the base, then gradually or abruptly decurved, tapering or clavate. *Lateral sepals* obliquely elliptic or oblong, acute. *Petals* erect, oblanceolate, oblong or pandurate, sometimes with a basal anticous lobe, upper margin flat or crenulate. *Labellum* a minute, linear organ in front of the column and adpressed to the stigma, fused to the column at the base. *Column*: anther thecae horizontal with upcurved upper portions; pollinia two, sectile; auricles large; stigma sessile on the front side of the column; rostellum two-lobed with lorate and concave lateral arms, bearing a globular viscidium each, central lobe minute, obsolete, rarely prominent (*B. coerulea* Harv. ex Lindl.). *Capsule* ribbed, oblong to cylindrical. **(HK, PL)**

Distribution (Fig. 8.2)

The seven *Brownleea* species occur in Africa, distributed mainly in the southern African summer-rainfall area and extending into tropical Africa and Madagascar. **(HK, PL)**

Phylogenetics

The genus was previously included in subtribe Disinae with which it shares the galeate, spurred median sepal and the basal fusion of the petals to the column (Linder 1986*a*; Dressler 1981). However, in *Brownleea* the petals are adnate to the dorsal sepal, the labellum fused to the base of the column, and the stigma derived from the median stigma lobe (Linder and Kurzweil 1994), which are characters found in subtribe Coryciinae. Consequently it was suggested that the genus may be of hybrid origin (Linder and Kurzweil 1994, 1996). In view of its problematic systematic affinities the genus was placed in its own subtribe.

Linder (1981*a*) revised the taxonomy of the genus. Linder and Kurzweil (1996) documented the detailed column structure and postulated a phylogeny based on an analysis of morphological data. Three well-defined clades can be recognized. Long, curving spurs are the synapomorphy of the *Brownleea macroceras* Sond. clade, whereas the *B. parviflora* Harv. ex Lindl. clade is characterized by dense inflorescences with small flowers and strongly decurved spurs. The *B. galpinii* Bolus clade is characterized by spurs that are equally long as the dorsal sepal and by apically widened petals, often with a crenulate margin.

An analysis based on sequence data from ITS ribosomal DNA (Douzery *et al.* 1999) corroborates these morphological results by excluding *Brownleea* from Disinae. **(HK, PL)**

Ecology

Brownleea occurs in the higher rainfall, montane-temperate areas. *Brownleea galpinii*, *B. recurvata* Sond., *B. mulanjiensis* H.P.Linder, *B. parviflora*, and *B. macroceras* are found in grasslands, whereas *B. coerulea* and *B. maculata* P.J.Cribb grow in forested habitats (the latter species occasionally as an epiphyte). The species flower comparatively late—at the end of summer—long after most other deciduous-terrestrial orchids in the area have flowered. **(HK, PL)**

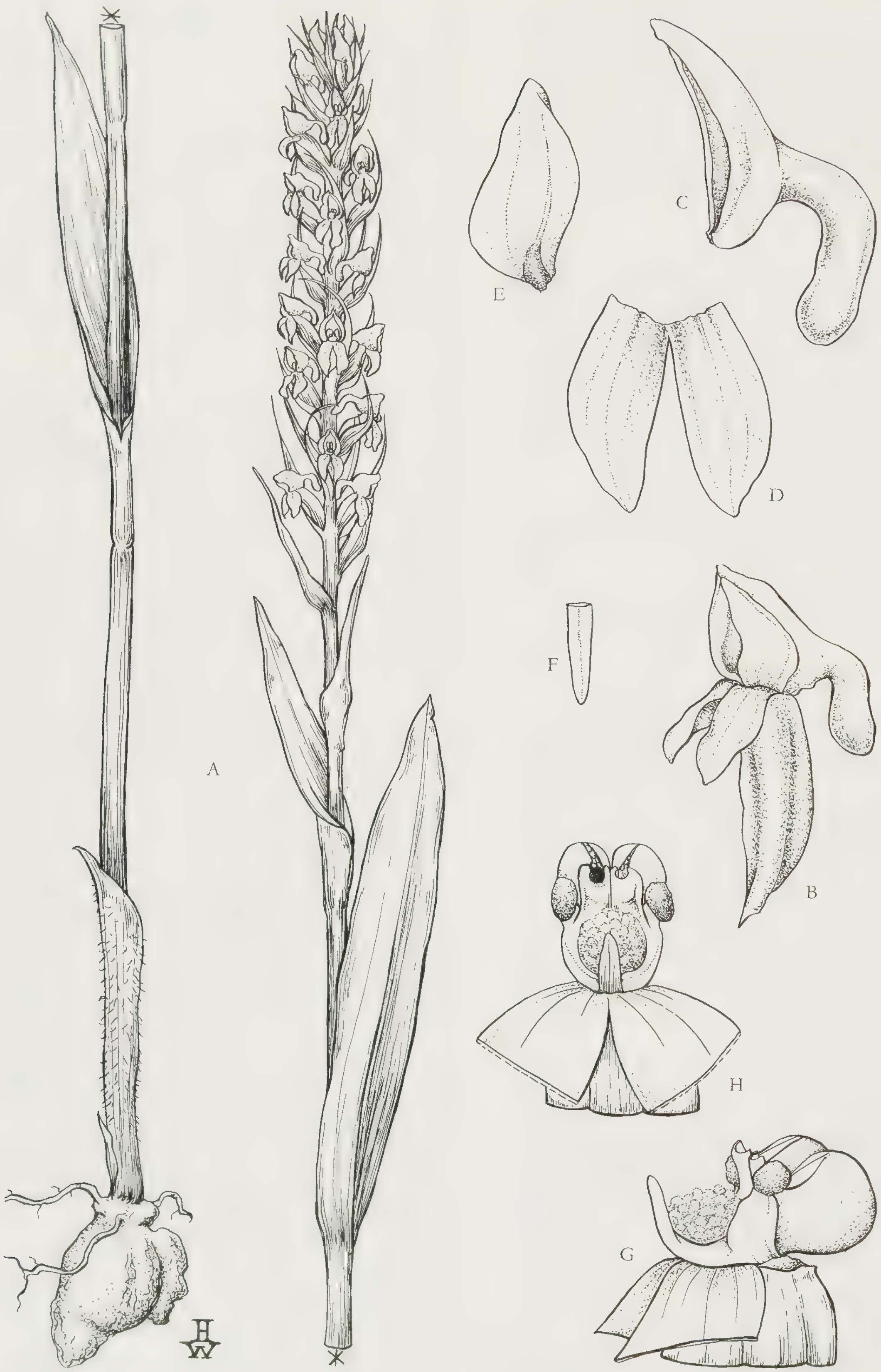


Fig. 8.1. *Brownleea parviflora* Harv. ex Lindl. A. Flowering plant, ×1; B. Flower, side view, ×5; C. Dorsal sepal, ×10; D. Lateral sepals, ×10; E. Petal, ×10; F. Labellum, ×20; G. Column, side view, perianth removed, ×20; H. Column, front view, perianth removed, ×20. Drawn by Heather Wood from *Milne-Redhead & Taylor 10326*.

Pollination

Information on the pollination biology of this genus remains incomplete. Long-tongued flies, *Prosoeca ganglbauri* (Nemestrinidae), carry pollinaria of *B. macroceras* at a site in the Drakensberg of South Africa (Johnson and Steiner 1995). Possible mimicry between the flowers of *B. galpinii* and *Cephalaria galpiniana* Szabo subsp. *simplicior* B. L. Burtt (Dipsacaceae) in the Drakensberg was suggested by Hilliard and Burtt (1981). **(SJ)**

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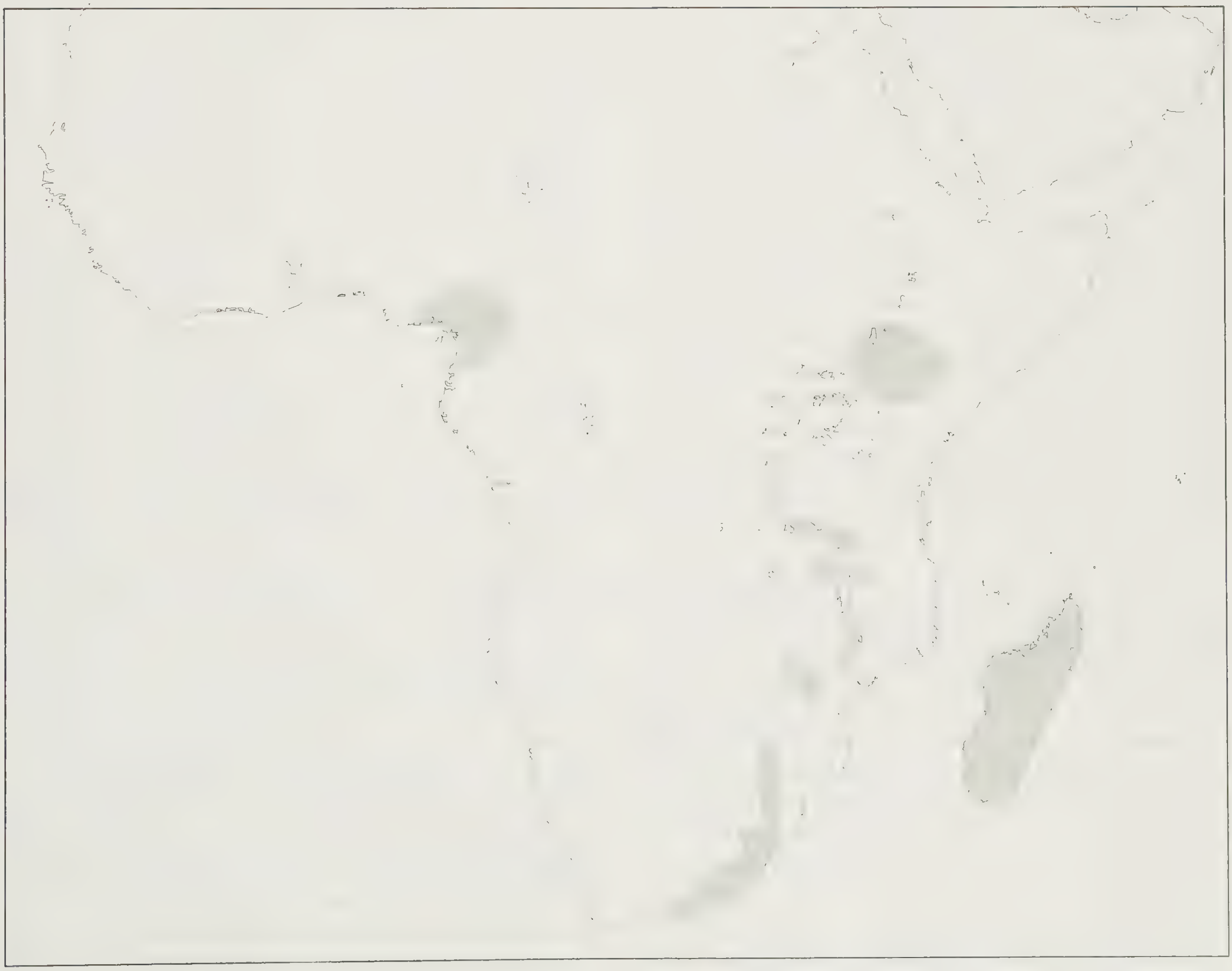

Fig. 8.2. Distribution map of *Brownleea.*

SUBTRIBE CORYCIINAE

Coryciinae Benth., *Genera Plantarum*, **3**, 464 (1883), as Corycieae. Type: *Corycium* Sw.

Description

Terrestrial *herbs* with root tubers and slender to stout stems, mostly with glabrous above-ground parts. *Leaves* cauline, clustered in the lower stem portion, linear, lanceolate, or ovate. *Inflorescence* a terminal raceme, lax or dense, with few–many flowers. *Flowers* resupinate or not. *Dorsal sepal* adnate to the *petals* and forming a galea with them. *Labellum* fused to the column at the base, mostly with an appendage which is often larger than the lip blade. *Column* without prominent stalk; anther horizontally reflexed or pendent, thecae often widely separated at the far corners of a long horseshoe-shaped connective; pollinia two, sectile; stigma one or two slightly convex pads, ontogenetically derived from the median carpel. **(HK, PL)**

Distribution (see map for *Disperis*)

Coryciinae are a primarily African group of about 123 species in five genera. *Ceratandra* and *Evotella* are endemic to the Western Cape of South Africa. *Pterygodium* and *Corycium* are also mainly southern African in distribution and range into tropical Africa. *Disperis* is widespread in southern and tropical Africa and also represented in Asia with a few species. **(HK, PL)**

Phylogenetics

The monophyly of Coryciinae *s.l.* is supported by two morphological characters: a two-lobed lip appendage and the rostellum with spreading and elongate lateral arms (Linder and Kurzweil 1994). In addition, the monophyly of Coryciinae, Brownleeinae, and Huttonaeinae is based on the unusual character of the stigma being derived from the median carpel apex. However, this character is variable in *Brownleea* (Linder and Kurzweil 1996). The morphological evidence for Coryciinae *s.l.* therefore appears to be persuasive. However, this clade is not retrieved in parsimony analyses of nuclear ribosomal DNA ITS sequences (Douzery *et al.* 1999).

Ceratandra, *Evotella*, *Pterygodium*, and *Corycium* are distinct from *Disperis* and have been termed Coryciinae *sensu stricto* (Kurzweil *et al.* 1991). The latter group is clearly monophyletic, defined by several column and pollen characters (Linder and Kurzweil 1994). In the detailed study by Kurzweil *et al.* (1991) two clades within the Coryciinae *s.s.* were distinguished. Synapomorphies of the *Ceratandra-Evotella* clade are the equally long cauline leaves and an anchor-shaped or broadly triangular lip. An entire lip appendage and a rostellum which is strap-like define the *Pterygodium-Corycium* clade. **(HK, PL)**

Pollination

Coryciinae have been described as having some of the most 'bizarre' floral structures in the orchids (Kurzweil *et al.* 1991), yet the function of these complicated structures, until recently, has remained obscure. Much of the unusual variation in floral morphology in this group can be linked directly to its pollination biology. Most, if not all, of the species secrete floral oil and are pollinated by solitary oil-collecting bees in the genus *Rediviva* (Melittidae) (K. Steiner, unpublished). Southern African species of *Disperis* are pollinated primarily by oil-collecting bees, but in the rest of Africa and on other continents they must be pollinated by other insects as they do not appear to secrete oil (Steiner 1989; Manning and Linder, 1992). The production of oil as a pollinator reward is rare among orchids in general and is known outside of southern Africa only among unrelated Neotropical species in the genera *Ornithocephalus*, *Zygostates*, *Oncidium*, and *Sigmatostalix* (Vogel 1974; Dressler 1993). The bees that pollinate flowers of these species are unrelated to southern African oil-collecting bees.

Rediviva is a small group of highly specialized bees that collect oil to serve as a food source, together with pollen, for their developing larvae. They use their specially modified forelegs to scrape up and hold the oil until they transfer it to their hind legs for the flight back to the nest. The collection of oil with the forelegs, rather than the tongue, reflects the use of oil solely as a food source for the larvae and not as a food source that is ingested by the adult bee. It also explains why many oil-secreting orchids (e.g. *Disperis* and *Corycium*) have two openings to the flower, two pollinaria (i.e. one for each foreleg), and two well-separated stigma lobes (e.g. *Disperis*, *Corycium*, and *Pterygodium*). The exception to this are the twin spurred flowers of *Satyrium*, which are visited by insects or birds in search of nectar rather than oil (Johnson 1996*a*, *b*, 1997*a*, *b*).

In many Coryciinae (e.g. *Disperis* and *Corycium*), one pollinarium is deposited on each foreleg as the bee withdraws its legs from the flower after rubbing for oil (Steiner 1989). These pollinaria then contact the stigma lobes in the next flower as the bee inserts its legs to collect additional oil. In *Pterygodium* and *Ceratandra*, pollinaria are deposited on other parts of the bee's body, such as the middle legs, hind legs, or the ventral tip of the abdomen. This differential placement of pollinaria allows one bee to pollinate different oil-secreting orchids flowering synchronously in the same habitat. Even on a single part of the bee (e.g. the foreleg), pollinaria from three different species of *Disperis* and one species of *Corycium* may be carried at the same time without interfering with each other (Steiner 1989, 1993; K. Steiner, unpublished). Thus, the number of *Rediviva* species that pollinate oil-secreting orchids is much smaller than the total number of orchid species, despite the specialized nature of the oil bee–oil flower relationship (K. Steiner, unpublished).

Like their South American counterparts, oil secretion in the Coryciinae can be either from trichome elaiophores or from epithelial elaiophores (Vogel 1974; K. Steiner, unpublished). In *Disperis*, all but one of the species have either trichome or verrucate elaiophores (Steiner 1989). *Pterygodium*, on the other hand, has mostly epithelial elaiophores, whereas *Evotella*, *Corycium*, and *Ceratandra* have only epithelial elaiophores (K. Steiner, unpublished). In all Coryciinae, oil is secreted primarily from the lip appendage. This explains the elaborate development of this structure in many of the genera including *Disperis*, *Corycium*, *Evotella*, and *Pterygodium*. In

Ceratandra, oil is secreted from a special gland on the lip blade known as the callus (Steiner 1998). The evolutionary loss of the callus in the clade that includes *C. grandiflora* Lindl. and *C. globosa* Lindl. is associated with a switch from pollination by oil bees to pollination by monkey beetles (Steiner 1998).

Although oil-secreting orchids are dependent on *Rediviva* bees for pollination, most *Rediviva* bees are more dependent on oil-secreting Scrophulariaceae (e.g. *Diascia* and *Ixianthes*) than they are on orchids (Steiner 1989; Steiner and Whitehead 1990, 1991, 1996). Many *Rediviva* species show obvious adaptations for collecting oil from their Scrophulariaceae host plants, but no such adaptations can be identified for the exploitation of oil from orchids. This indicates that the evolution of oil secretion in southern African orchids not only occurred after the evolution of oil secretion in the Scrophulariaceae but also developed opportunistically with respect to the pre-existing relationship between *Rediviva* and Scrophulariaceae.

Disperis is the only member of the Coryciinae in which most (*c.* 80%) of the species lack an obvious floral reward. One such rewardless species is *Disperis capensis* (L.f.) Sw., endemic to the western Cape. Its flowers mimic the nectar-rich flowers of *Polygala bracteolata* L. and are pollinated by the carpenter bee, *Xylocopa rufitarsus* (Johnson 1994). *Disperis capensis* is the only non-rewarding species for which pollination information is available. It is likely that most of the other non-rewarding species also rely on some form of mimicry to attract pollinators (Steiner 1989).

Most Coryciinae are dependent on oil-collecting bees for pollination, but some species have become facultatively or obligately autogamous. Only two of the oil-secreting *Disperis* species, *D. thorncroftii* Schltr. and *D. paludosa* Harv. ex Lindl., are known to self-pollinate (Steiner 1989), but among the non-rewarding species, especially those with small flowers (i.e. *D. bodkinii* Bolus, *D. macowanii* Bolus, *D. woodii* Bolus, *D. disaeformis* Schltr., and possibly *D. micrantha* Lindl.), facultative or obligate autogamy is probably the norm. *Disperis bodkinii* is not only autogamous, but in some populations it is cleistogamous (Manning and Linder 1992). Cleistogamy is the only form of self-pollination in *Pterygodium,* found in two species, *P. connivens* Schelpe and *P. newdigatae* Bolus (Duthie 1915; Stewart *et al.* 1982).

Ceratandra species are predominantly outcrossing, but self-pollination occurs under rare circumstances in *C. atrata* (L.) Dur. & Schinz and quite commonly in *C. globosa* (Steiner 1998). In both cases, pollinia drop down onto the receptive stigma while the caudicle and viscidium remain attached to the rostellum arms. *Corycium* species are also predominantly outcrossing, but some species are facultatively autogamous in at least some populations. *Corycium carnosum* (Lindl.) Rolfe is predominantly outcrossing when pollinators are present, but if they are absent it may be facultatively self-pollinating (K. Steiner, unpublished). *Corycium nigrescens* Sond. is outcrossing through much of its range in the Drakensberg, but self-pollinating in at least one population in the southern Cape (Steiner, unpubl.). *Corycium flanagani* (Bolus) Kurzweil & H. P. Linder, a rare plant on the high mountains of the Drakensberg, is occasionally outcrossed by oil-collecting bees but regularly self-pollinates in the absence of pollinators (K. Steiner, unpublished). **(KS)**

9. CERATANDRA

Ceratandra Eckl. ex Bauer, *Ill. Orch. Pl.*, **4**, t. 16 (1837). Type species: *Ceratandra atrata* (L.) T. Durand & Schinz.

Ceratandropsis Rolfe, *Fl. Cap.*, **5** (3), 266 (1913). Type: *C. grandiflora* (Lindl.) Rolfe.

Evota (Lindl.) Rolfe, *Fl. Cap.*, **5** (3), 268 (1913).

Derivation of name

From the Greek *keras*, horn, and *aner*, *andros*, man, referring to the horn-like thecae-canals of the type species. **(HK, PL)**

Description (Plate 2; Fig. 9.1)

Slender or robust terrestrial *herbs*, with a cluster of thick roots, some species apparently perennating with small root tubers. *Stems* up to 45 cm tall, occasionally up to four in a bundle. *Leaves* mostly dimorphic, consisting of few–many equally long linear leaves all along the stem and a rosette of linear or narrowly lanceolate radical leaves. *Inflorescence* terminal, lax or dense, with few or many flowers; bracts narrowly triangular, acute, glabrous or sometimes marginally ciliate, slightly shorter to slightly longer than the ovary. *Flowers* resupinate or not, mostly in various shades of yellow, often tinged with red or orange, sometimes flowers pink and white. *Dorsal sepal* lanceolate, mostly connate with the petals. *Lateral sepals* spreading or slightly reflexed, elliptic, obtuse to subacute. *Petals* spathulate, obtuse, or acute. *Labellum* with an anchor-shaped or semi-circular blade, unspurred, appendiculate or not, often with a small laminal callus. *Column* with a short undifferentiated stalk; anther pendent, thecae mostly adjacent and somewhat diverging, with the two tapering canals sticking upward, in one species thecae widely separated; pollinia two, sectile; stigma lobes ovate to elliptic, slightly convex, basal at the rostellar arms (due to the anther reflexion on the dorsal side of the column), ontogenetically derived from the median carpel; rostellum flat, partly covering the thecae. **(HK, PL)**

Distribution (Fig. 9.2)

Ceratandra comprises six species endemic to the western and southern parts of the Cape Floristic Region (South Africa). **(HK, PL)**

Phylogenetics

The genus *Ceratandra* is distinct and monophyletic, defined by its cluster of thick, furry roots surrounded by a common sheath (Kurzweil *et al.* 1995), as well as by the lip and anther shape (Kurzweil *et al.* 1991). *Ceratandra bicolor* Sond. and *C. harveyana*, both with resupinate flowers and a prominent two-lobed lip appendage, were previously segregated as the genus *Evota* (Rolfe 1913; Stewart *et al.* 1982). However, their generic separation does not appear justified as the species are clearly linked with the other *Ceratandra* species by the

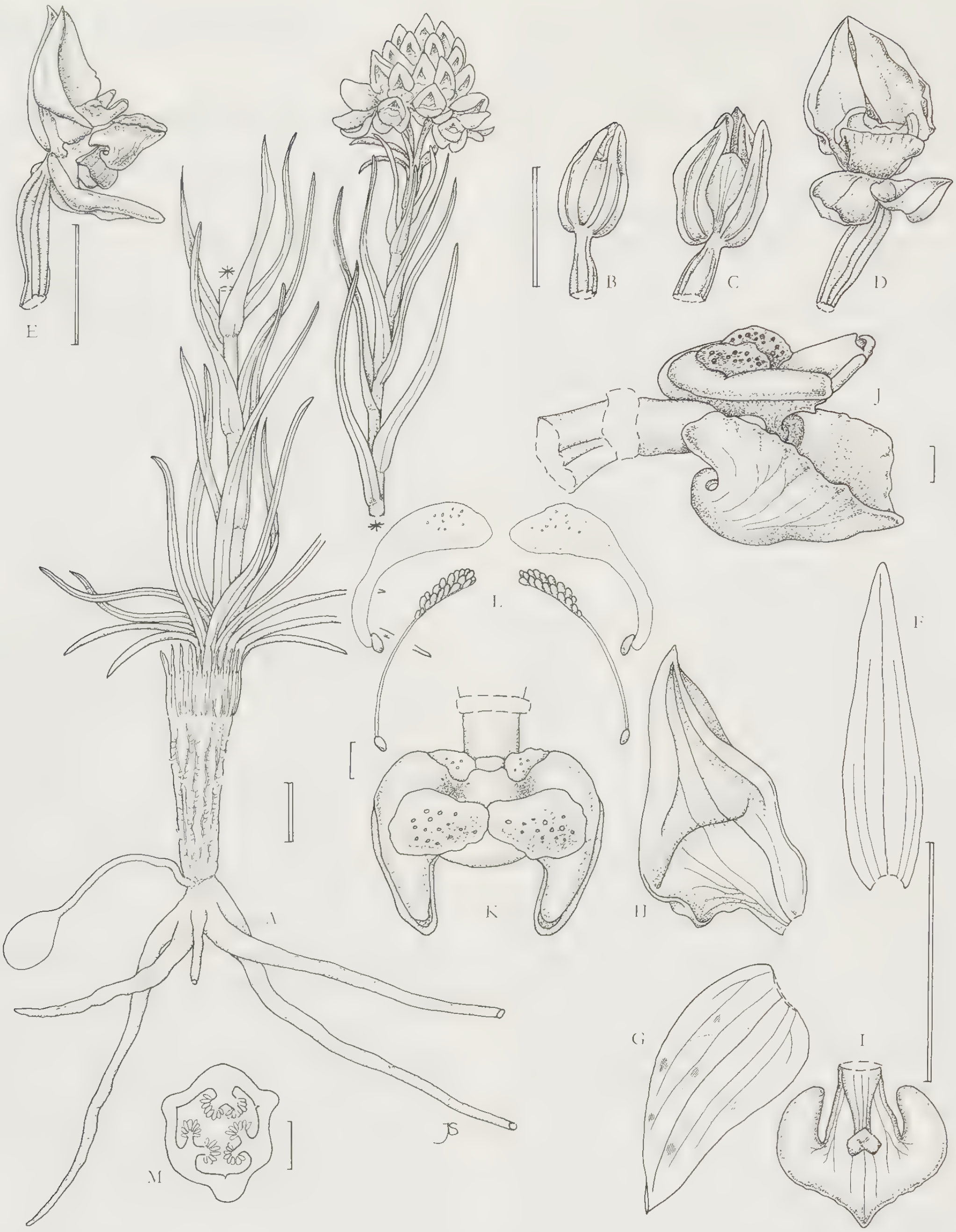

Fig. 9.1. *Ceratandra grandiflora* Lindl. A. Habit; B. Young bud; C. Bud; D. Flower, front view; E. Flower, side view; F. Dorsal sepal; G. Lateral sepal; H. Petal; I. Labellum, with callus; J. Column and labellum, side view; K. Column, from above; L. Pollinarium; M. Ovary, transection. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Cutting 1433* and Kew Spirit Collection no. 27850.

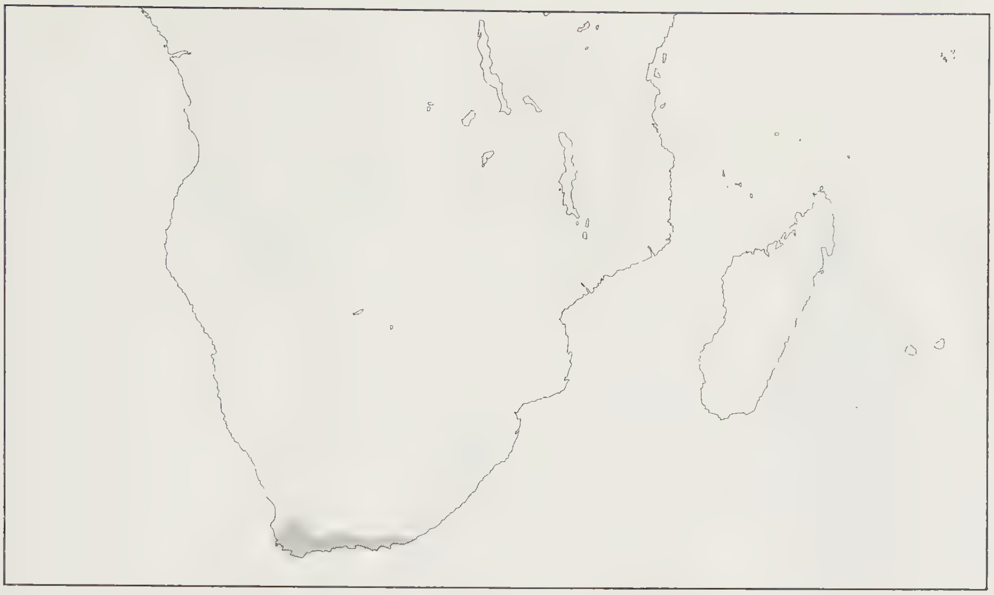

Fig. 9.2. Distribution map of *Ceratandra.*

lip shape, the linear cauline leaves, and the presence of a basal cluster of narrow leaves; as a result they have therefore been reduced to a section of *Ceratandra* (Kurzweil *et al.* 1991). *Ceratandra venosa* has a complicated taxonomic history and has at times been placed in *Corycium* and *Pterygodium.* The species was recently included in *Ceratandra* but placed in a monospecific section (Kurzweil *et al.* 1991).

In the past tubers were sometimes thought to be absent in *Ceratandra.* However, recent studies have shown that small tubers deeply buried in the soil exist in some specimens, indicating that the unusual underground organ of *Ceratandra* is not a completely new development but merely a variation of the tuberous type (Kurzweil *et al.* 1995). (**HK, PL)**

Ecology

Ceratandra species inhabit marshes or seepages in the mountains of the western and southern parts of the Cape Floristic Region, partly near sea level and at low elevations (*C. grandiflora*, *C. venosa*), partly at higher elevations (*C. atrata*, *C. bicolor*, *C. globosa* Lindl., *C. harveyana*). Flowering in all species is stimulated by fire, and burning of their habitat can lead to a sudden mass flowering (particularly in *C. atrata*). Flowering takes place in spring in the lowlands or early summer at higher elevations. (**HK, PL)**

Pollination

See above under Coryciinae.

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10. CORYCIUM

Corycium Sw., *Kongl. Vetensk. Acad. Nya Handl.*, ser. **2**, **21**, 220 (1800). Type species: *Corycium orobanchoides* (L.f.) Sw. (lecto.).

Derivation of name

From the Greek *korys*, helmet, and Latin *-ium*, quality or nature of, referring to the helmet-shaped hood. (**HK, PL)**

Description (Plate 3; Fig. 10.1)

Slender or robust terrestrial *herbs*, herbaceous, glabrous, with testicular tubers. *Stem* up to 55 cm tall, unbranched, with few hyaline leaf sheaths below the foliage leaves. *Foliage leaves* few or many, cauline and clustered in the lower portion of the stem, lanceolate or narrowly lanceolate, green at anthesis or rarely withered. *Inflorescence* terminal and dense spike, with many flowers; bracts lanceolate, as long as the flowers to slightly longer. *Flowers* numerous, resupinate or rarely not, green, white, yellow, mauve or purple or combinations of these. *Sepals* fresh or sometimes black and dry in the open flowers. Dorsal sepal normally connate with the petals and forming a hood with it, mostly elliptic. Lateral sepals free or fused in different degrees, pendent or reflexed, ovate or nearly so. *Petals* obliquely ovate and often strongly concave or saccate. *Labellum* fused to the

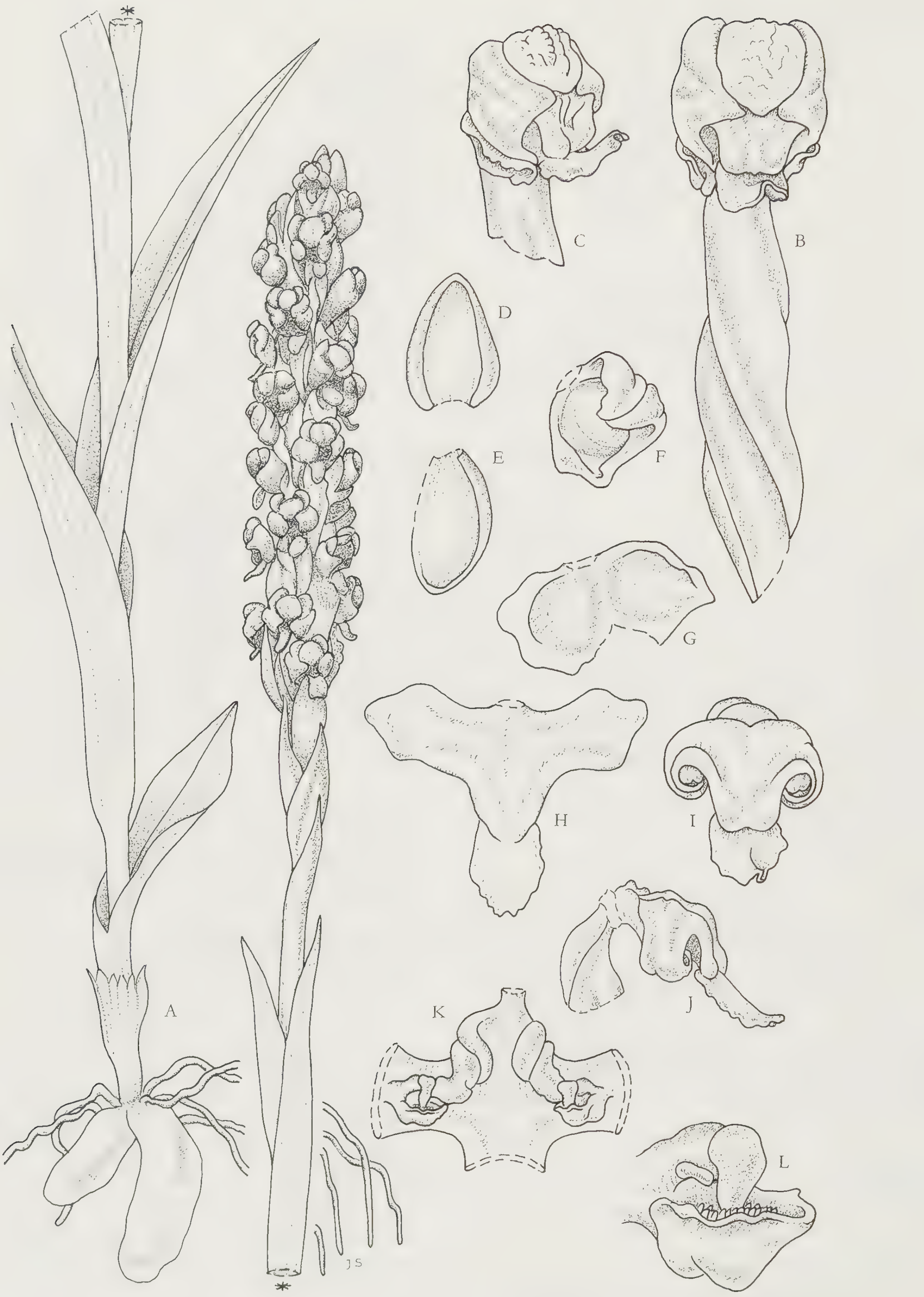

Fig. 10.1. *Corycium dracomontanum* Parkman & Schelpe. A. Habit, ×1; B. Flower, front view, ×4; C. Flower, side view (ovary removed), ×4; D. Dorsal sepal, ×4; E. Lateral sepal, ×4; F. Petal, ×4; G. Petal, opened out, ×4; H. Column and labellum, opened out, ×4; I. Column and labellum, front view, ×4; J. Column and labellum, side view, ×4; K. Column from below, ×4; L. Pollinarium, ×14. Drawn by Judi Stone from photographs and *Kurzweil 1492*.

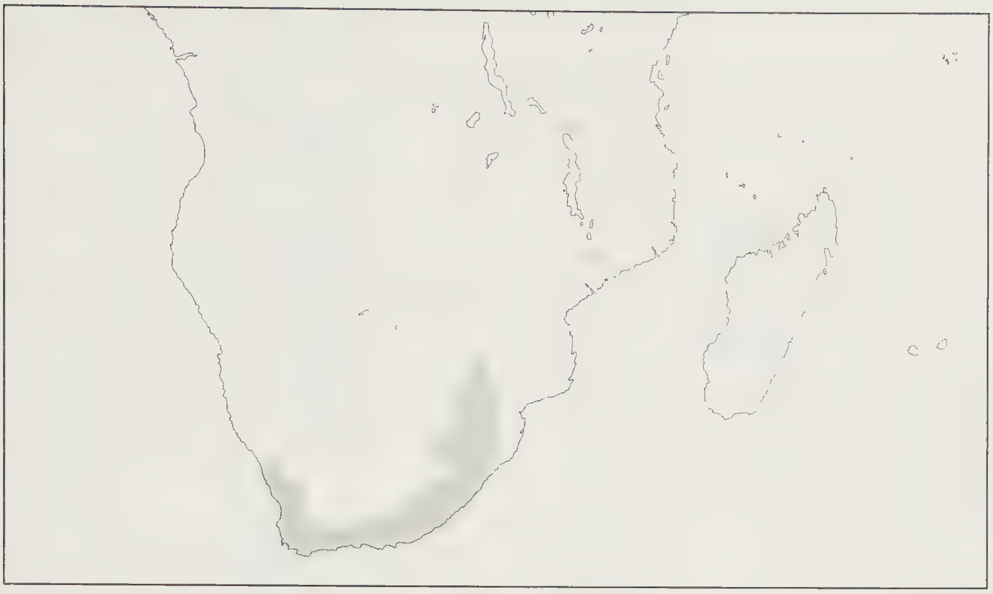

Fig. 10.2. Distribution map of *Corycium*.

column base, blade bilobed or rarely lanceolate, lip appendage normally shield-like with various processes and more or less horizontal, rarely suberect and elongate. *Column* without an undifferentiated stalk, complicated in its structure, variously twisted and contorted; anther thecae situated on the far corners of an elongate horseshoe-shaped connective; pollinia two, sectile; stigma as two convex pads situated on the rostellum and ontogenetically derived from the median carpel; rostellum a narrow strap of tissue, with two lateral arms holding the viscidia. **(HK, PL)**

Distribution (Fig. 10.2)

The genus comprises 14 species in southern Africa. Centres of diversity are the northern and western Cape as well as the Drakensberg in the eastern Cape and KwaZulu-Natal. *Corycium nigrescens* Sond. and the related *C. dracomontanum* Parkman & Schelpe were recently recorded in Malawi and southern Tanzania (Kurzweil 1992; Cribb and Kurzweil 1994). (**HK, PL)**

Phylogenetics

Corycium shares a number of features with *Pterygodium*, indicating that the two genera are closely related. However, *Corycium* is clearly distinct in its dense inflorescences and the globose or semi-globose flowers of most of its species. Douzery *et al.* (1999) included a single species of *Pterygodium* and four species of *Corycium*. They found *Pterygodium* to be nested within *Corycium*, thus casting doubt on the monophyly of *Corycium* as circumscribed here.

A phylogeny of the species based on morphological data was published by Kurzweil *et al.* (1991). *Corycium carnosum*, with its hood-like and beaked lip appendage and the stigmas on the rostellum arms, is apparently isolated and placed in the monospecific section *Carnosum*. A suberect or erect elongate lip appendage with a keel on the ventral side defines the *C. flanaganii* (Bolus) H. Kurzweil & H. P. Linder clade, which was formally recognized as section *Microglossum*. *Corycium flanaganii* has open flowers and seems to be phylogenetically isolated (Kurzweil *et al.* 1991). This species, which has non-resupinate flowers, was segregated as the genus *Anochilus* together with two species (*P. hallii* (Schelpe) Kurzweil & H.P.Linder, *P. inversum* (Thunb.) Sw.) now thought to belong to the genus *Pterygodium* (Rolfe 1913; Stewart *et al.* 1982). Most species of the genus belong to the *C. crispum* Sw. clade, which is the most distinct clade within *Corycium*. The clade was formally recognized as section *Corycium* and is characterized by a clawed and shield-like lip appendage with lateral processes.

Two species, currently known as *Evotella rubiginosa* (Sond. ex Bolus) H. Kurzweil & H.P.Linder and *Pterygodium magnum* Rchb.f., have been included in *Corycium* in the past (Rolfe 1913; Stewart *et al.* 1982) but are different from *Corycium* in critical characters (Kurzweil *et al.* 1991). (**HK, PL)**

Ecology

The habitat preferences of *Corycium* species are diverse. In the Cape Floristic Region most species are found in sandy soil in fynbos. Flowering in some species is stimulated by fire (*C. carnosum*, *C. excisum* Lindl., *C. bicolorum* (Thunb.) Sw.). *Corycium carnosum* is found in mountain marshes in the western Cape of South Africa. Two species (*C. deflexum* (Bolus) Rolfe, *C. ingeanum* E.G.H.Oliv.) occur in arid scrubland along the western fringes of the Karoo in the northern Cape Province of South Africa. In contrast, the summer-rainfall region species *C. tricuspidatum* Bolus, *C. nigrescens*, *C. dracomontanum*, *C. flanaganii*, and *C. alticola* Parkman & Schelpe grow in grassland. The species flower after or during the rains, which is in spring in the winter-rainfall area and in summer further north.

Corycium species normally occur scattered or in groups of 20–30 plants. *Corycium orobanchoides* Sw. sometimes forms more extensive and dense colonies and is often found in disturbed sites such as road verges. **(HK, PL)**

Pollination

See above under Coryciinae.

Taxonomic literature

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Swartz, O. (1800). Orchidernes slagter och acter upstallde. *Kongl. vetenskaps academiens nya handlingar*, **21**, 202–54.

11. DISPERIS

Disperis Sw., *Kongl. Vetensk. Acad. Nya Handl.*, **21**, 218 (1800). Type species: *Disperis circumflexa* (L.) T. Durand and Schinz.

Dryorkis Thouars, *Nov. Bull. Soc. Philom.* n. 19, 31b (1809). Type species: not designated.

Dryopeia Thouars, *Hist.*, t. 1–3 (1822). Type species: not designated.

Dipera Spreng., *Syst. Veg.*, 676 (1826). Type species: not designated.

Derivation of name

From the Greek *dis*, double, and *pera*, pouch, referring to the saccate lateral sepals of this genus. **(HK, PL)**

Description (Plate 4; Fig. 11.1)

Slender terrestrial *herbs*, with ovoid root tubers, up to 65 cm tall. *Stems* unbranched, glabrous or hairy, often with reddish or purplish tinge. *Foliage leaves* one to few, soft-herbaceous, occasionally reduced, basal or cauline, alternate or opposite, glabrous or rarely pubescent, lanceolate, ovate or orbicular, entire, sometimes purple underneath. *Inflorescence* with one to many flowers, racemose, subcorymbose or secund; bracts similar to the cauline leaves; ovary twisted. *Flowers* resupinate, white, yellow or in various shades of pink or red. *Dorsal sepal* adnate to the petals, sometimes with a spur; lateral sepals spreading or reflexed, spurred or saccate. *Petals* falcate. *Labellum* basally fused with the column, with narrow claw; blade varied in shape, smooth, verrucose or pubescent, always with entire or two-lobed appendage. *Column* sessile or with an insignificant stalk; anther mostly horizontal with adjacent and parallel thecae; pollinia two, sectile; auricles small, sculptured; stigma singly and bilobed or consisting of two separate areas, positioned either at the front of the column or dorsal on the rostellum (sometimes at the base of the lateral rostellum arms); rostellum tripartite, with variously shaped and twisted arms projecting forward and apically bearing the viscidia, and a central rostellum lobe which is flat and covers both thecae. **(HK, PL)**

Distribution (Fig. 11.2)

Disperis comprises about 84 species in southern and tropical Africa. Approximately 21 species are found in Madagascar, the Mascarenes, and the other Indian Ocean islands. In addition the genus ranges into Asia; one or two species are each endemic to India, Thailand, China, the Philippines, the Malay Archipelago, and New Guinea. **(HK, PL)**

Phylogenetics

There is no current infrageneric classification of the genus. Schlechter (1901) divided the genus into two sections: *Eu-Disperis* with alternate leaves and *Anaphyllum* Schltr. with opposite or subopposite leaves. However, this is clearly artificial.

Manning and Linder (1992) carried out a phylogenetic analysis of the genus *Disperis* based on morphological data of the South African species. The study showed two lineages in the genus, a mostly tropical clade and an almost exclusively southern African clade. The tropical group is characterized by a bilobed lip appendage and baculate pollen exine and is distributed in Asia and tropical to subtropical Africa.

Three species have the southernmost limit of distribution in southern Africa (*D. johnstonii* Rolfe, *D. anthoceros* Rchb.f., *D. virginalis* Schltr.). The southern African clade has an entire lip appendage and pollen grains with a rugulate exine. Centres of diversification are the western Cape of South Africa and the Drakensberg. The southern African clade seems to have radiated through existing guilds of oil-secreting flowers (Manning and Linder 1992). The tropical species have consistently simple rostellum arms, but the variation in their shape and orientation is greater in the southern African species. The character of the rostellum arms proved to be a reliable way of assessing relationships among the species. The different rostellum forms are related to the placement of the pollinia on different parts of the insect. **(HK, PL)**

Ecology

Most species in the genus *Disperis* prefer forested habitats, ranging from rain forests to montane cloud forests (tropical Asia and

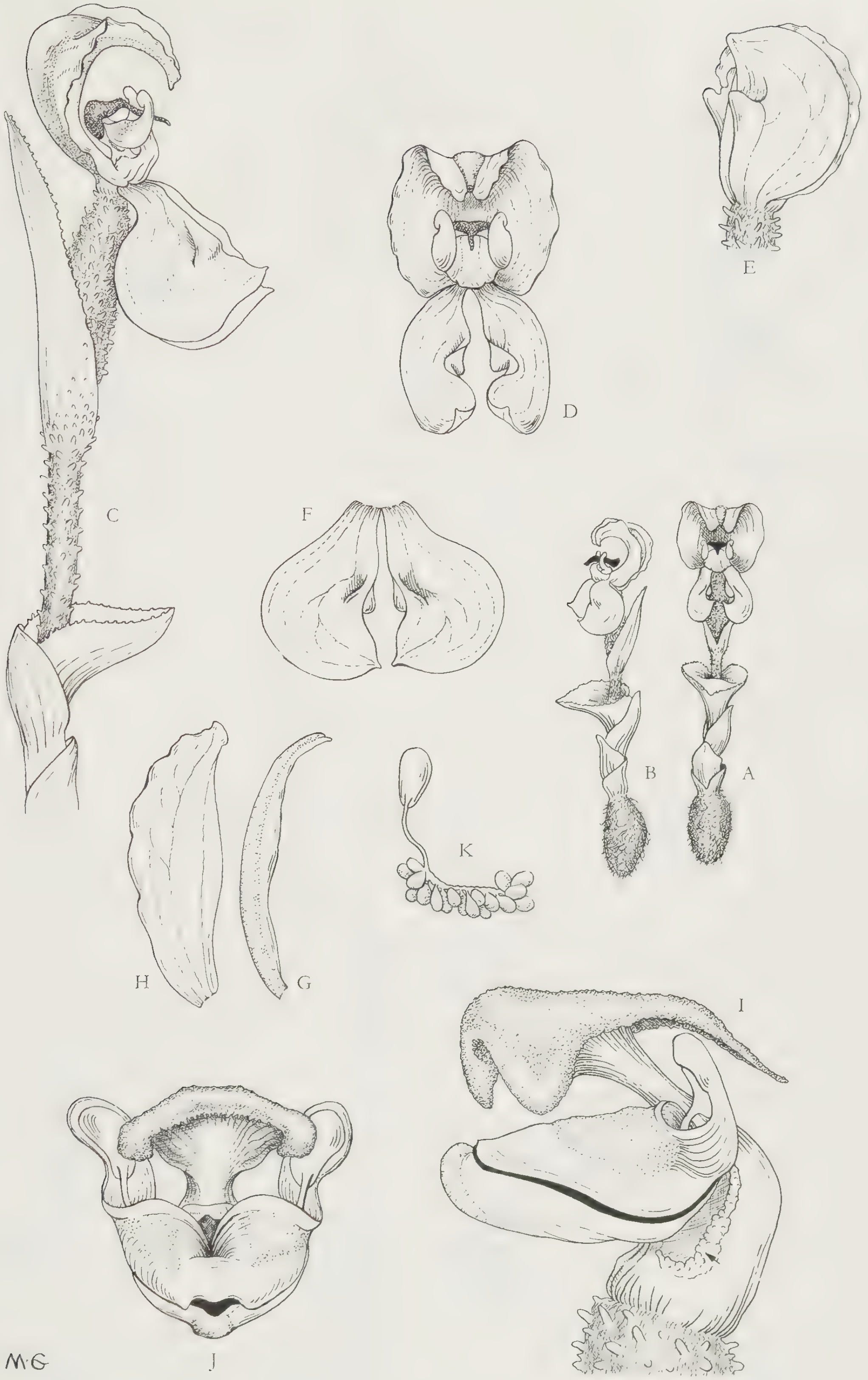

Fig. 11.1. *Disperis pusilla* Verdc. A. Habit, front view, ×1.5; B. Habit, side view, ×1.5; C. Habit, side view, ×4; D. Flower, front view, ×4; E. Flower in bud, ×4; F. Lateral sepals, ×4; G. Dorsal sepal, side view, ×4; H. Petal, ×4; I. Labellum and column, side view, ×14; J. Labellum and column, front view, ×14; K. Pollinium, ×14. Drawn by Mary Grierson from *Richards 7159*.

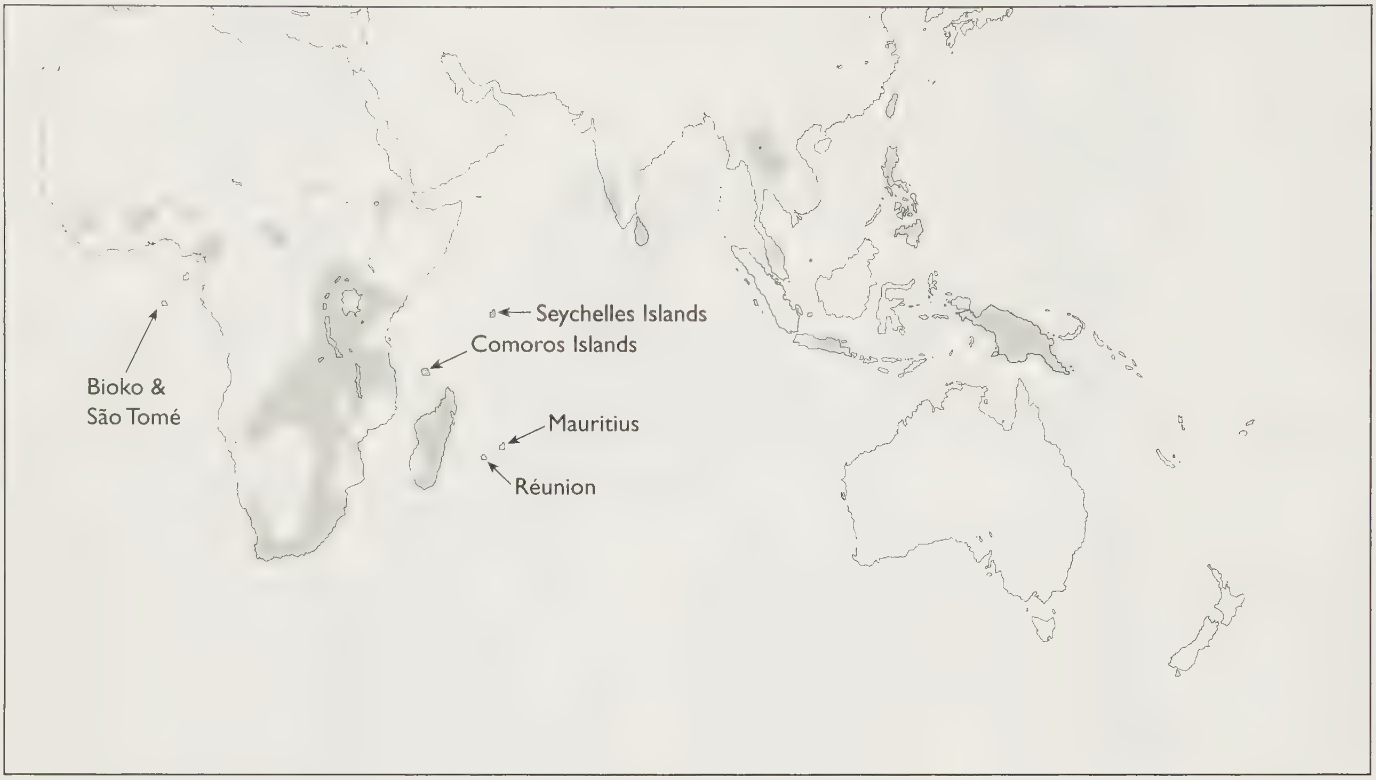

Fig. 11.2. Distribution map of *Disperis.*

Africa) and cool temperate forests (South Africa, as far south as the eastern Cape). However, in South Africa the genus has diversified in its habitat preferences. Several species have evolved into more open habitats; examples are marshes (*D. paludosa* Harv. ex Lindl.; western Cape), fynbos (*D. capensis* Sw., *D. cucullata* Sw., *D. bodkinii* Bolus; western Cape), grassland (*D. renibractea* Schltr., *D. cardiophora* Harv., *D. stenoplectron* Rchb.f.; north-eastern provinces of South Africa), and karroid arid scrub (*D. purpurata* Rchb.f.; northern Cape of South Africa). As in other South African terrestrial orchids, extreme fire dependence is also found in the genus *Disperis*, although this is rare (*D. paludosa*). Whereas several species may be found growing in clumps of 20 or 30 plants, others are usually found growing singly or in smaller groups. Extensive colonies are rare in the genus (sometimes in *D. cardiophora* and *D. fanniniae* Harv.). In eastern Africa, colonies of several *Disperis* species, which are difficult to find in native vegetation, may occur in cypress (*Cupressus*) plantations where most other herbaceous plants cannot survive in the low light and deep leaf litter (Leedal and Cribb 1977). The flowering time of African *Disperis* species is just after the rains, i.e. in spring in the South African winter-rainfall area and in summer in the rest of the area. **(HK, PL)**

Pollination

See above under Coryciinae.

Taxonomic literature

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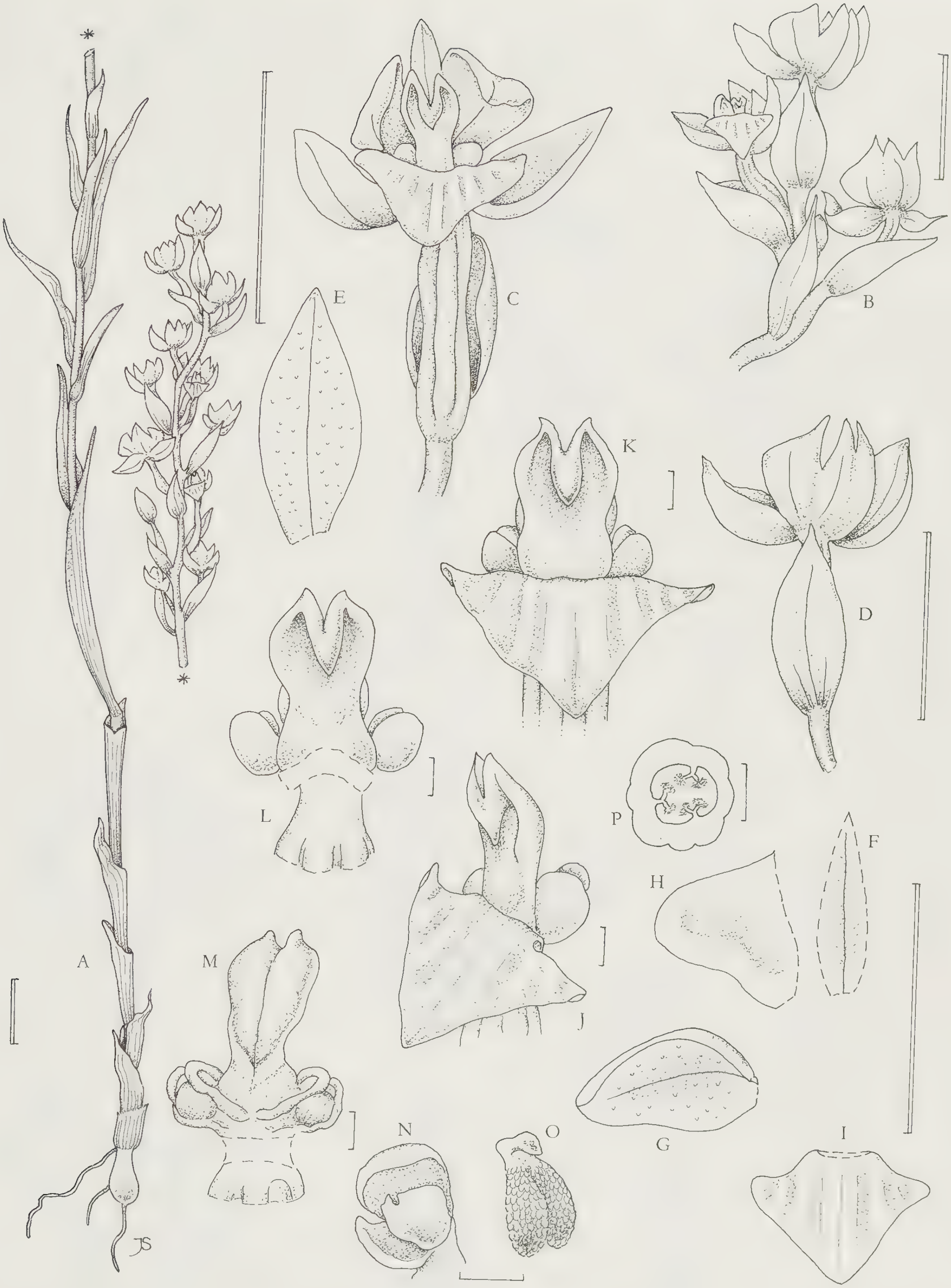

Fig. 12.1. *Evotella rubiginosa* (Sond. ex Bolus) Kurzweil & H. P. Linder. A. Habit; B. Inflorescence; C. Flower, front view; D. Flower, back view; E. Bract; F. Dorsal sepal; G. Lateral sepal; H. Petal; I. Labellum; J. Labellum and column, side view; K. Labellum and column, front view; L. Column, front view; M. Column, back view; N. Anther cap; O. Pollinarium; P. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Zeyher 3946*.

12. EVOTELLA

Evotella Kurzweil & H.P.Linder, *Pl. Syst. Evol.*, **175**, 215 (1991).
Type species: *Evotella rubiginosa* (Sond. ex Bolus) Kurzweil & H. P. Linder.

Derivation of name

After the genus *Evota* (Greek *eu*, well, *ous*, *otos*, ear) and the diminutive suffix, *-ella*. **(HK, PL)**

Description (Plate 5; Fig. 12.1)

Slender or robust terrestrial *herbs*, glabrous in all above-ground parts, with root tubers. *Stems* unbranched, with hyaline leaf sheaths below the foliage leaves. *Leaves* cauline, linear-lanceolate, acute. *Inflorescence* terminal, dense, many flowered. *Flowers* resupinate, open cup-shaped, white and maroon. *Dorsal sepal* adnate to the petals, lanceolate. *Lateral sepals* spreading. *Labellum* broadly triangular, patent, obtuse-acute, with entire but apically bifid lip appendage with a pendent apical process. *Column* without undifferentiated stalk, thecae semi-pendent, widely separated; pollinia two, sectile; stigmas two, positioned on the terminal rostellum portions; viscidia terminal on the rostellum, on both sides of the lip appendage. **(HK, PL)**

Distribution (Fig. 12.2)

Evotella is a monospecific genus from the western Cape of South Africa, with *E. rubiginosa* as its sole species. **(HK, PL)**

Phylogenetics

Evotella rubiginosa was previously placed in *Corycium* (Rolfe 1913; Stewart *et al.* 1982) or *Pterygodium* (Schlechter 1898), which is a reflection of its complicated taxonomic history. In contrast, Kurzweil *et al.* (1991) showed the clear affinities of this genus with *Ceratandra*, namely by the broadly hastate lip and the equally long cauline leaves and suggested that *Evotella* and *Ceratandra* are closely related. Nevertheless, the unlobed lip appendage is unknown in the *Ceratandra* clade and supports the recognition of *Evotella* as a separate genus. **(HK, PL)**

Ecology

Evotella rubiginosa is found flowering in spring in fynbos after fire. **(HK, PL)**

Pollination

See above under Coryciinae.

Taxonomic literature

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Schlechter, R. (1898). Monographie der Disperideae. *Bulletin d' Herbier Boissier*, ser. **1**, **6**, 800–21, 846–59, 905–55.
Stewart, J., Linder, H. P., Schelpe, E. A., and Hall, A. V. (1982). *Wild orchids of southern Africa.* Macmillan south Africa, Johannesburg.

13. PTERYGODIUM

Pterygodium Sw., *Kongl. Vetensk. Acad. Nya Handl.*, ser. **2**, **21**, 217 (1800). Type species: *Pterygodium alatum* (Thunb.) Sw.
Ommatodium Lindl., *Gen. Sp. Orch. Pl.*, 365 (1838). Type species: *O. volucris* (L.f.) Lindl.
Anochilus Rolfe, *Fl. Cap.*, **5** (3), 280 (1913), *pro parte*; Stewart *et al.*, *Wild Orch. S. Afr.*, 189 (1982), *pro parte.* Type species: *A. inversum* (Thunb.) Rolfe.

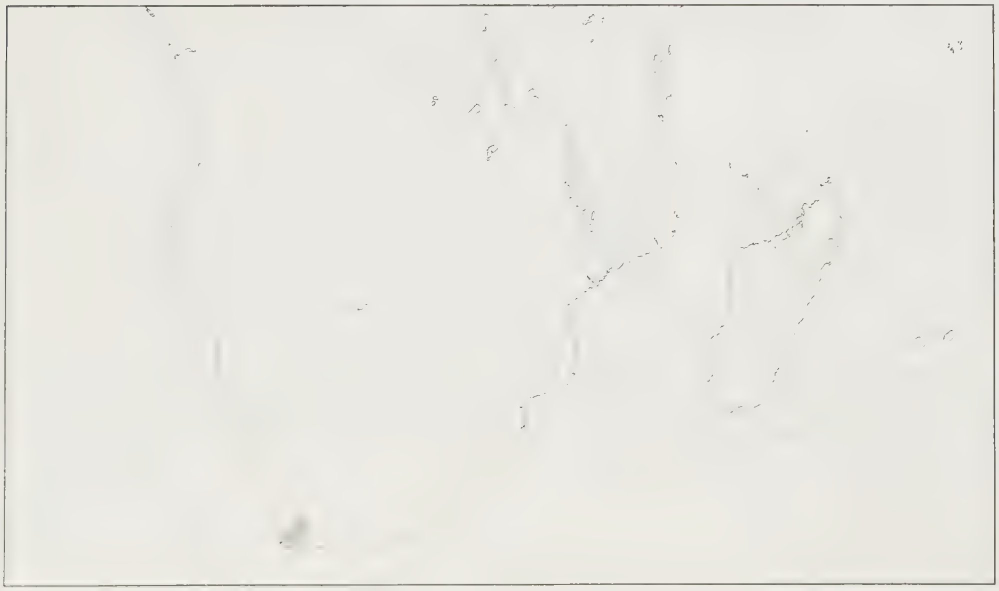

Fig. 12.2. Distribution map of *Evotella.*

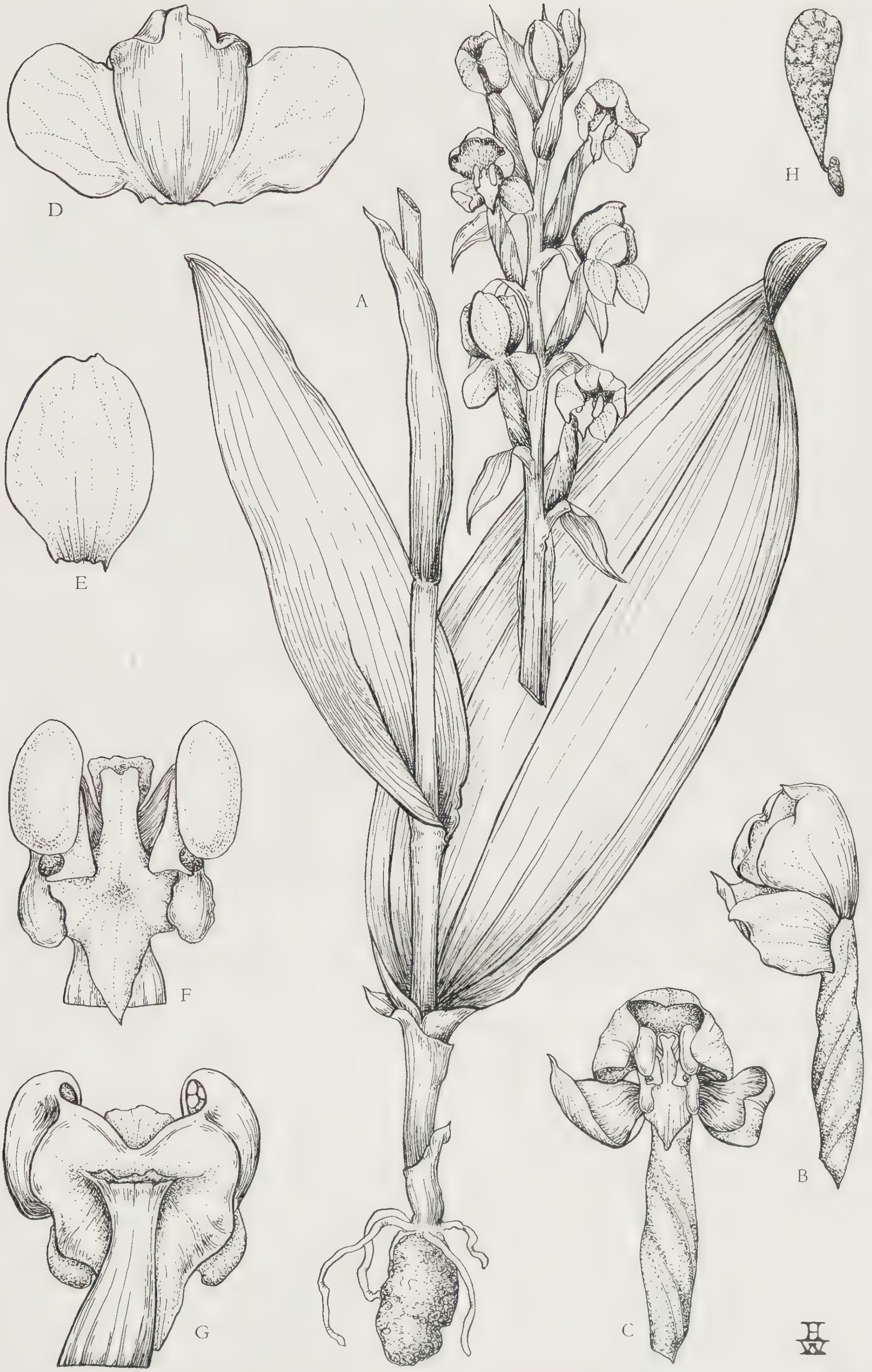

Fig. 13.1. *Pterygodium ukingense* Schltr. A. Flowering plant, ×1; B. Flower, side view, ×3; C. Flower, front view, ×3; D. Dorsal sepal and petals, ×4; E. Lateral sepal, ×4; F. Labellum and column, front view, sepals and petals removed, ×5; G. Labellum and column, back view, sepals and petals removed, ×5; H. Pollinium, ×10. Drawn by Heather Wood from *Stolz 2609*.

Derivation of name

After the Greek *pteron*, wing, and the suffix *-odes*, denoting likeness, referring to the spreading lateral sepals. (**HK**, **PL)**

Description (Plate 6; Fig. 13.1)

Slender or robust terrestrial *herbs*, glabrous in all above-ground parts, with testicular tubers. *Stem* unbranched, up to 1.5 m tall, with leaf sheaths below the foliage leaves. *Foliage leaves* few to many, rarely one, cauline, clustered near the stem base if many, lanceolate to linear-lanceolate, acute. *Inflorescence* terminal, lax to dense, unbranched, few–many flowered, rarely with a single flower; bracts ovate to elliptic, basal sheathing. *Flowers* resupinate or not, generally with a comparatively shallow hood, pale green to yellow, rarely white, sometimes with red or purple tinges. *Dorsal sepal* adnate to the petals, lanceolate, occasionally subapically saccate. *Lateral sepals* spreading, rarely reflexed, lanceolate. *Petals* subrotund or variously lanceolate, entire or crenulate. *Labellum* diverse in shape, linear, deltate, three or two-lobed, rarely marginally fringed, always with an elongate and unlobed but sometimes funnel-shaped and hollow appendage. *Column* without an undifferentiated stalk, thecae parallel but far apart on each side of the labellum appendage, thecae horizontal or rarely erect; pollinia two, sectile; stigma in the form of two convex pads situated on the rostellum close to the median line or on the lateral arms, ontogenetically derived from the median carpel; rostellum an elongate strap of tissue between the two anther thecae. (**HK**, **PL)**

Distribution (Fig. 13.2)

Pterygodium comprises 17 species in South Africa and Lesotho and one species (*P. ukingense*) endemic to southern Tanzania. In southern Africa, the greatest diversity is found in the western Cape Province, and several of the western Cape species range into the northern and eastern Cape Province. Another centre of diversity is found in the Drakensberg in KwaZulu-Natal where four species are found. (**HK**, **PL)**

Phylogenetics

In the phylogenetic analysis by Kurzweil *et al.* (1991), *Pterygodium* comprises two clades. The clade including sections *Magnum* and *Ommatodium* is characterized by reflexed bracts, which serve as a synapomorphy for the group. A species currently recognized as *P. volucris* was separated into a new genus *Ommatodium* by Rolfe (1913) because of its erect anthers. The sole species of section *Magnum*, *Pterygodium magnum*, was included in the genus *Corycium* (Stewart *et al.* 1982), but the cup-like flowers and the shape of the lip appendage indicate a relationship to *Pterygodium* (Kurzweil *et al.* 1991). Sections *Anochilus* and *Pterygodium* are defined by a solid lip appendage. In the past the two species of the former section were separated into the genus *Anochilus* on the basis of the superior lip (Rolfe 1913; Stewart *et al.* 1982), together with an apparently unrelated species currently included in *Corycium* (as *C. flanaganii*). Most species are included in section *Pterygodium*, which is defined by few cauline leaves and lax inflorescences with few flowers. (**HK**, **PL)**

Ecology

Species of the genus *Pterygodium* grow in fynbos in the Cape Floristic Region of South Africa and montane grassland in the southern African summer-rainfall area. Although most prefer areas with comparatively high rainfall, *P. hallii* (Schelpe) H. Kurzweil & H. P. Linder, *P. schelpei*, and *P. volucris* are known from the fringes of the Karoo in the western and northern Cape Provinces of South Africa. Most species are known from low to medium elevations, but *P. platypetalum* Lindl. is known only from higher mountain slopes. Unlike other southern African terrestrial orchids, flowering of *Pterygodium* species is not strongly stimulated by fire. However, the flowering of *P. catholicum* Sw. is clearly enhanced by previous

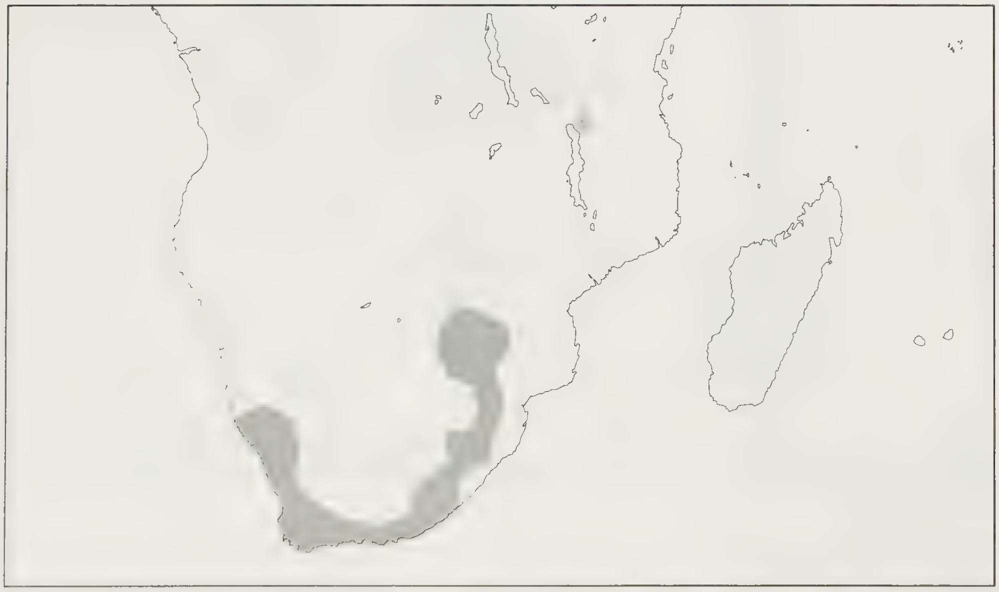

Fig. 13.2. Distribution map of *Pterygodium.*

burning of its habitat. In this species, a large number of non-flowering plants can usually be found around flowering individuals in old veld (i.e. veld that has not been burned recently). The species flower just after the rains, in spring in the western Cape and in summer farther north.

Most *Pterygodium* species grow either singly and scattered or are found in populations of 20–50 plants. *Pterygodium catholicum* and *P. alatum* (Thunb.) Sw. usually form fairly dense colonies and are believed to multiply vegetatively. *Pterygodium* species are commonly found on the richer, heavier soils derived from shale, whereas *Disa* species are commonly seen on the more oligotrophic, sandstone-derived soils. **(HK, PL)**

Pollination

See above under Coryciinae.

Taxonomic literature

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Swartz, O. (1800). Orchidernes slagter och acter upstallde. *Kongl. vetenskaps academiens nya handlingar*, **21**, 202–54.

SUBTRIBE DISINAE

Disinae Benth., *Genera Plantarum*, **3**, 464 (1883), as Diseae. Type: *Disa* Bergius.

Description

Robust or slender *herbs* with root tubers, mostly glabrous, sometimes with sterile shoots. *Leaves* radical, basal or cauline, usually narrowly lanceolate or linear. *Inflorescence* a terminal raceme with few to many flowers, rarely subcapitate or one-flowered. *Flowers* resupinate or not. *Sepals* often apiculate, brightly coloured; dorsal usually hood-like and spurred; laterals spreading or more or less reflexed. *Petals* simple or structurally modified, exserted from the dorsal sepal galea or included in it, undivided but apically often bifid, lorate, lanceolate, falcate or ovate, often with a basal anticous lobe, basally fused to the column. *Labellum* mostly narrow, rarely ovate, occasionally marginally fringed, rarely with unifacial apical tooth, always unspurred. *Column* without a prominent stalk; anther horizontal or rarely pendent, frequently with fairly elongate thecae; pollinia two, sectile, with two viscidia, rarely only with one; stigma pedicellate, tripulvinate; rostellum three-lobed or rarely unlobed. **(HK, PL)**

Distribution (see map for *Disa*)

The group comprises approximately 168 species currently placed in two genera. The large genus *Disa* is widespread in Africa as far as southern Arabia and on the Indian Ocean islands of Madagascar and Réunion, whereas *Schizodium* is endemic to the western, northern, and eastern Cape Provinces of South Africa. **(HK, PL)**

Cytogenetics

Cytological studies in Disinae are largely confined to *D. uniflora* and related species of *D.* section *Disa*, which are frequently seen in cultivation (Wimber 1987; Cywes and Pienaar 1990); the most common diploid number is 36. The same chromosome number was also found in *D. stairsii* Kränzl. (Hedberg 1977). Chromosome numbers of $2n = 40$ have been found in *D. sagittalis* (L.f.) Sw. and *D. uncinata* Bolus (Cywes and Pienaar 1990). **(HK, PL)**

Phylogenetics

Schizodium is reasonably distinct from *Disa* to be justified as a separate genus (Linder and Kurzweil 1994). Several of the groups within *Disa* have been segregated as separate genera in the past (*Amphigena*, *Orthopenthea*, *Penthea*, *Herschelia* = *Herschelianthe*, *Monadenia*; Rolfe 1912–1913, Linder 1981*b*, *c*, *d*, *e*, *f*), but recent evidence shows that their removal may render *Disa* paraphyletic. This would indicate that they are better retained in *Disa* until more information has become available. A more detailed discussion is presented below in the treatment on *Disa*.

Schizodium has as synapomorphies the pandurate lip and the flexuose, nitid stem (Linder 1986*a*). *Disa* has as a synapomorphy the completely deflexed lip. It is patent from the base, whereas in *Schizodium*, *Satyrium*, and Coryciinae the lip is erect at the base (continuing the direction of the ovary). **(HK, PL)**

14. DISA

Disa Bergius, *Descr. Pl. Cap.*, 348 (1767). Type species: *Disa uniflora* Bergius.

Penthea Lindl., *Gen. Sp. Orch. Pl.*, 360 (1838). Type species: *Penthea patens* (L.f.) Lindl.

Herschelia Lindl., *Gen. Sp. Orch. Pl.*, 362 (1838). Type species: *Herschelia coelestis* Lindl.

Monadenia Lindl., *Gen. Sp. Orch. Pl.*, 356 (1838). Type species: not designated.

Herschelianthe Rauschert, *Feddes Repert.*, **94**, 434 (1983). Type species: *Herschelia coelestis* Lindl.

Forficaria Lindl., *Gen. Sp. Orch. Pl.*, 362 (1838). Type species: *Forficaria graminifolia* Lindl.

Orthopenthea Rolfe, *Fl. Cap.*, **5 (3)**, 179 (1912). Type species: *Orthopenthea bivalvata* (L.f.) Rolfe

Amphigena Rolfe, *Fl. Cap.*, **5 (3)**, 197 (1913). Type species: *Amphigena leptostachya* (Sond.) Rolfe.

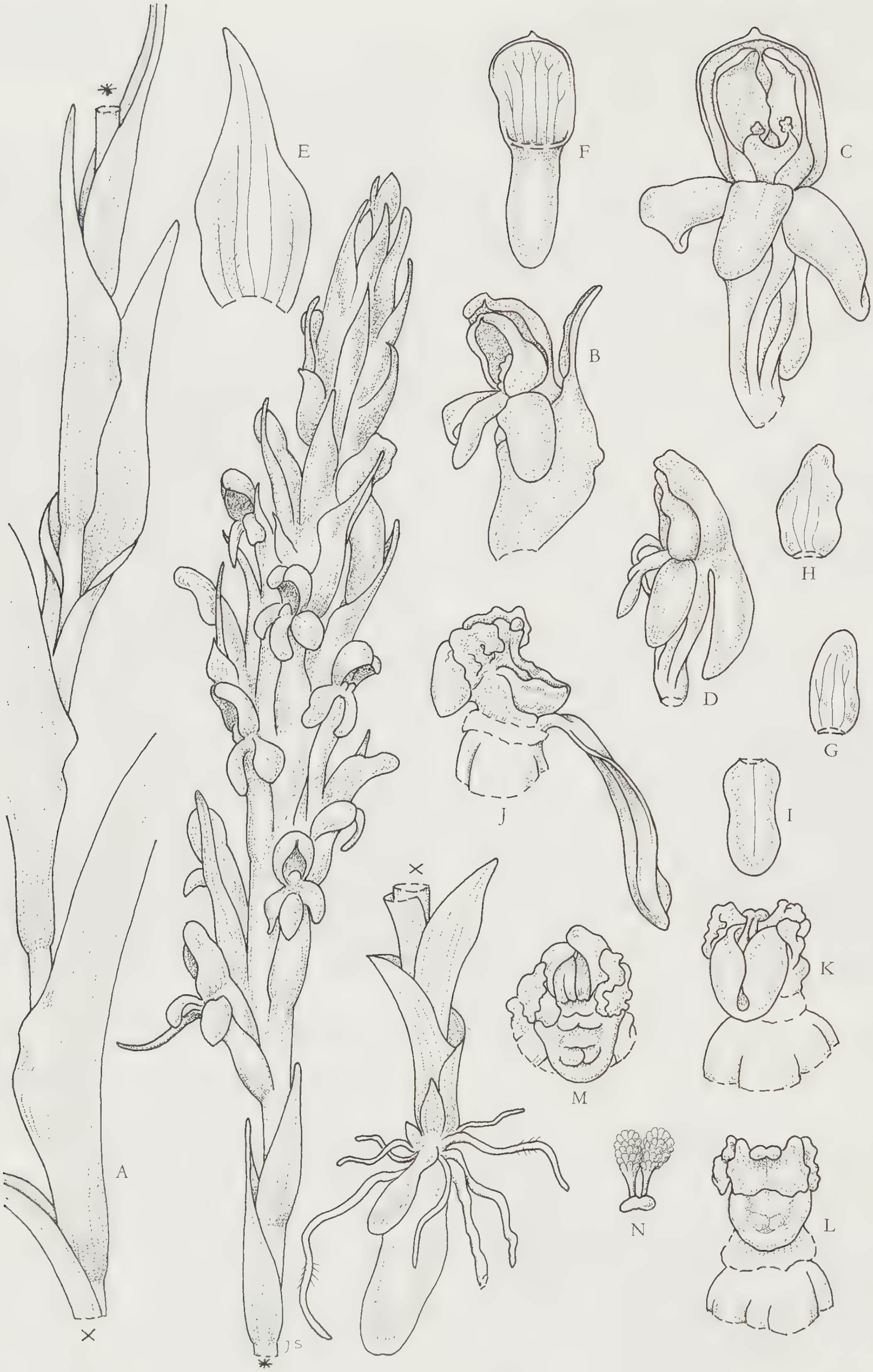

Fig. 14.1. *Disa brevicornis* (Lindl.) Bolus. A. Habit, ×1; B. Flower and bract, ×2; C. Flower, front view, ×3; D. Flower, side view, ×2; E. Bract, ×2; F. Dorsal sepal, ×2; G. Lateral sepal, ×2; H. Petal, ×2; I. Labellum, ×2; J. Labellum and column, side view, ×4; K. Column, back view, ×4; L. Column, front view, ×4; M. Column from above, pollinaria removed, ×4; N. Pollinaria, ×4. Drawn by Judi Stone from *Brummitt et al. 1982* and Kew Spirit Collection no. 27546.

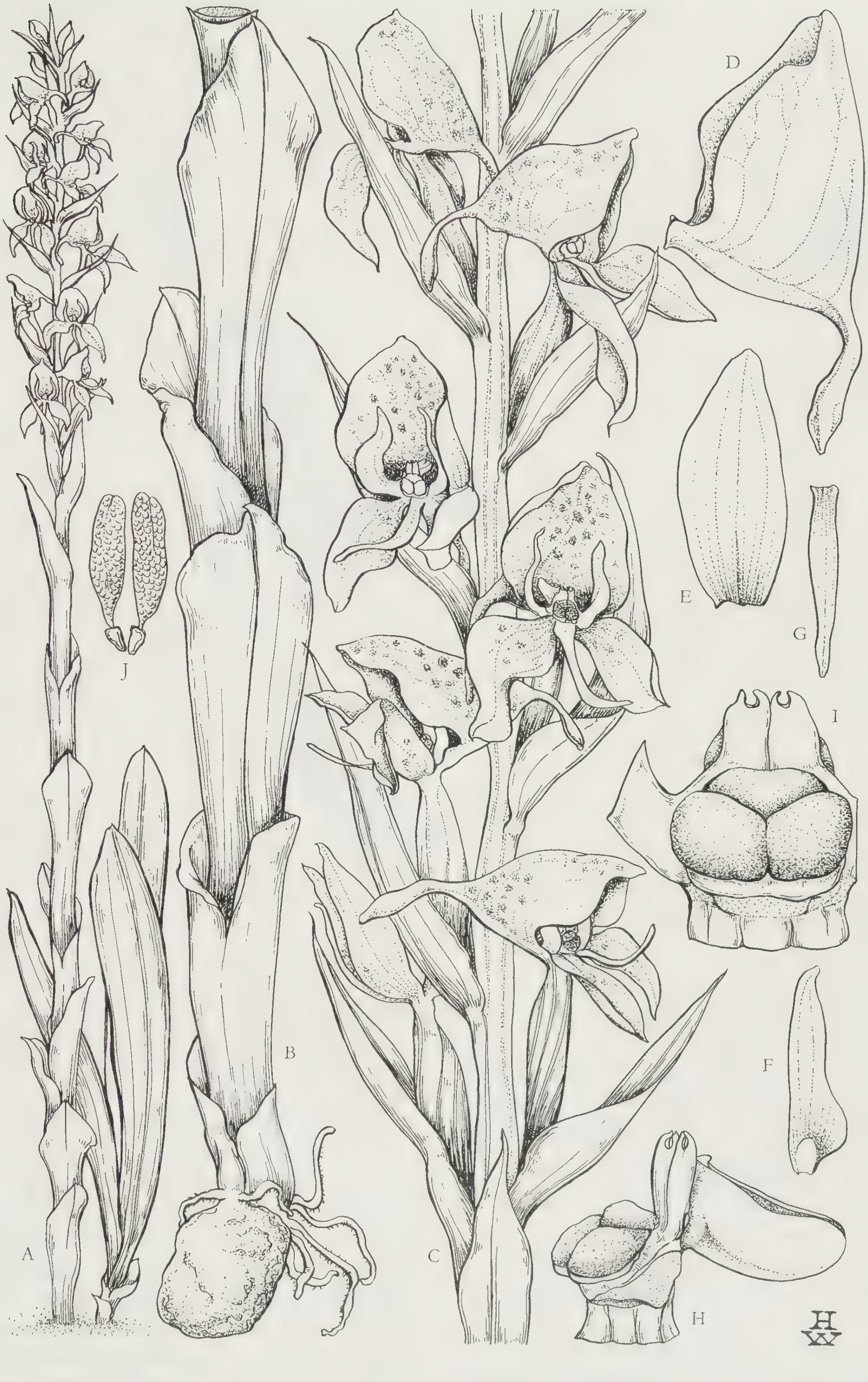

Fig. 14.2. *Disa walleri* Rchb.f. A. Habit, × 0.2; B. Lower part of stem, ×1; C. Lower part of inflorescence, ×1; D. Dorsal sepal, ×1.5; E. Lateral sepal, ×1.5; F. Petal, ×1.5; G. Labellum, ×1.5; H. Column, side view, sepals and petals removed, ×4; I. Column, front view, sepals and petals removed, ×4.5; J. Pollinia, ×3. Drawn by Heather Wood from *Polhill & Paulo 1371*.

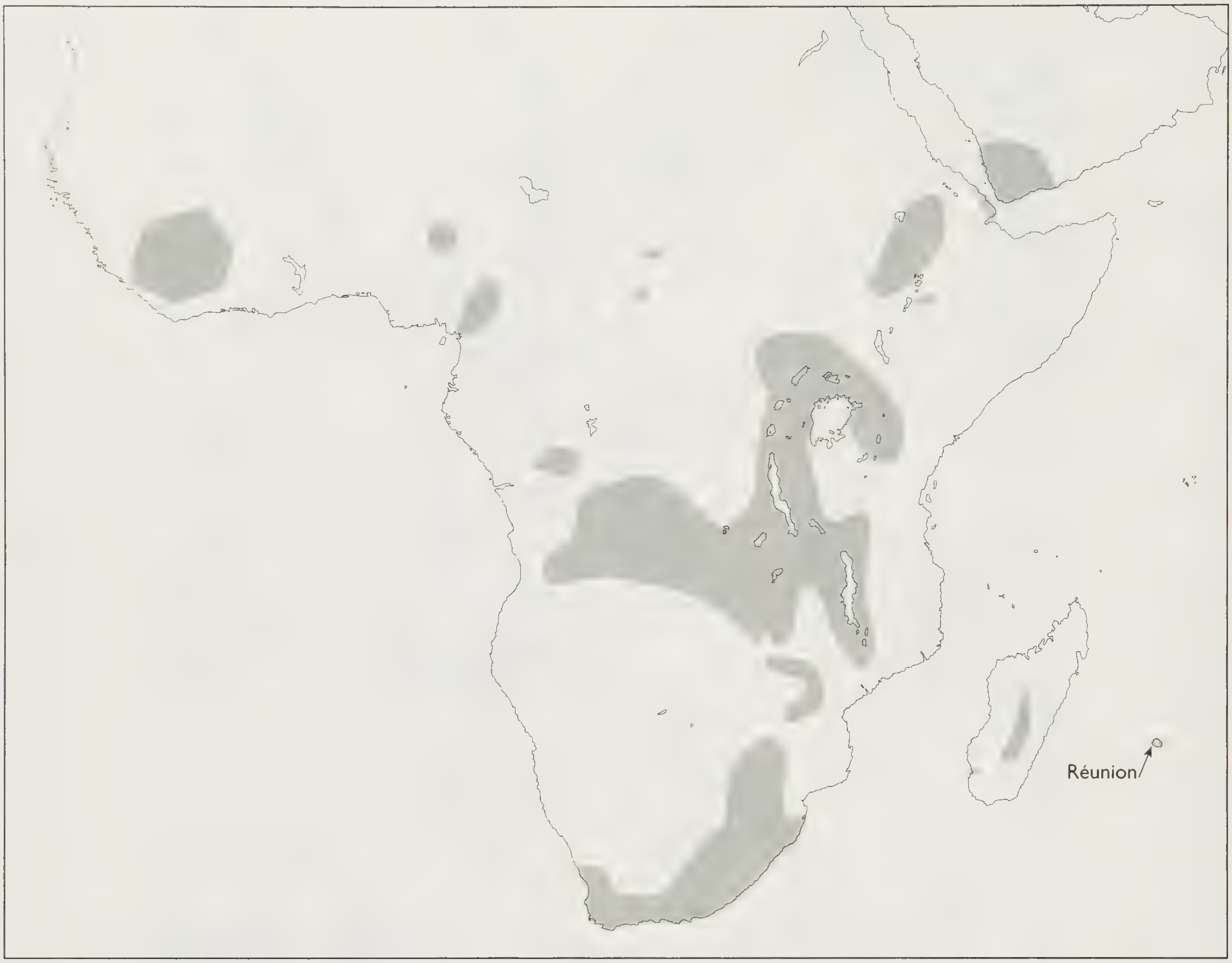

Fig. 14.3. Distribution map of *Disa.*

Derivation of name

The origin of the name *Disa* is controversial. Pettersson (1985) rejected the theory that the name is derived from the Greek *dives*, rich, alluding to the rich red colour of the first described species (*D. uniflora*). He suggested that it is more likely that the name refers to the mythical queen Disa, who arrived at the king's court wearing a fishnet to meet the challenge of being both dressed and undressed. This alludes to the reticulate pattern of the galea of the flower of the type species. **(HK, PL)**

Description (Plates 7, 8; Figs 14.1, 14.2)

Slender or robust terrestrial *herbs*, very rarely epiphytic or epilithic, usually glabrous; rarely with stolons, sometimes with sterile shoots. *Tubers* testicular, globose to elongate, villous. *Roots* mostly unbranched, comparatively few. *Stems* normally erect, unbranched, with hyaline basal sheaths above the tuber and apical sheaths which grade into the floral bracts. *Foliage leaves* radical, basal or cauline, linear to lanceolate, lax to imbricate, usually annual, soft-herbaceous to somewhat rigid, fresh at flowering time or sometimes hysteranthous; green but occasionally barred with red at the base, with red undersides, flushed with purple or entirely deep red; conduplicate or flat. *Inflorescence* a raceme or corymb, rarely one-flowered; bracts shorter or longer than flowers, lanceolate to ovate, acute or obtuse. *Flowers* resupinate or not. *Sepals* brightly coloured and often apiculate. Dorsal sepal galeate and frequently spurred; spur elongate or saccate, clavate, cylindrical or filiform, horizontal, curved upward or downward. Lateral sepals spreading or reflexed, flat or navicular. *Petals* oblong, structurally modified or very simple, tucked inside the dorsal sepal or exserted from it, erect or reflexed next to the anther, frequently with basal anticous lobe, sometimes twisted to obscure the galea entrance. *Labellum* unspurred, mostly linear or lorate, rarely ovate or spathulate, margins entire or rarely fringed. *Column* without prominent stalk; anther thecae mostly horizontal, rarely erect or pendent, adjacent and parallel, subglobose to elongate; pollinia two, sectile; auricles small; stigma cushion-like, tripulvinate, sessile or stipitate; rostellum normally three-lobed with two (sometimes connate) viscidia on the lateral arms, rarely unlobed with one viscidium. **(HK, PL)**

Distribution (Fig. 14.3)

The genus *Disa* as delimited here comprises about 162 species widespread in sub-Saharan Africa, with a few species extending to Madagascar and Réunion and one species on the Arabian Peninsula. The highest concentration of species is found in the Cape Floristic Region. (**HK, PL)**

Infrageneric treatment

1. **Disa** subgenus **Micranthae** (Lindl.) H.P.Linder, *Bothalia*, **16**, 56 (1986*b*). Type species: *D. chrysostachya* Sw. (lecto.).

Disa section *Micranthae* Lindl., *Gen. Sp. Orch. Pl.*, 348 (1838).

1.1. **Disa** section **Micranthae** Lindl., *Gen. Sp. Orch. Pl.*, 348 (1838); Linder, *Bull. Jard. Bot. Nat. Belg.*, **51**, 262 (1981*d*); Stewart *et al.*, *Wild Orch. S. Afr.*, 140 (1982); Linder and Kurzweil, *Orch. S. Afr.*, 193 (1999). Type species: *D. chrysostachya* Sw. (lecto.).

Characterized by the erect anther and the pendent spur on the dorsal sepal. The plants tend to produce sterile shoots, and the petals are frequently bilobed. This group of 23 species is mainly found in tropical grasslands.

2. **Disa** subgenus **Falcipetalum** H.P.Linder, *Contr. Bolus Herb.*, **9**, 30 (1981*c*). Type species: *D. longifolia* Lindl.

2.1. **Disa** section **Disella** Lindl., *Gen. Sp. Orch. Pl.*, 354 (1838); Linder, *Contr. Bolus Herb.*, **9**, 31 (1981*c*); Stewart *et al.*, *Wild Orch. S. Afr.*, 124 (1982); Linder and Kurzweil, *Orch. S. Afr.*, 199 (1999). Type species: *D. obtusa* Lindl. subsp. *obtusa* (lecto.).

The leaves are cauline and reach to the base of the dense inflorescence. The group is also characterized by the falcate petals and a short dorsal sepal spur. The section comprises 13 species, often found in damp black soils and flowering after fire. It is widely distributed in the Cape Floristic Region.

2.2. **Disa** section **Intermediae** H.P.Linder, *Contr. Bolus Herb.*, **9**, 65 (1981*c*); Stewart *et al.*, *Wild Orch. S. Afr.*, 128 (1982); Linder and Kurzweil, *Orch. S. Afr.*, 208 (1999). Type species: *D. galpinii* Bolus.

The plants are robust and have cauline leaves. Inflorescences are densely cylindrical with small to medium-sized flowers. The species are also characterized by falcate and broadly ovate petals. Two species in the eastern Cape and KwaZulu-Natal (South Africa).

2.3. **Disa** section **Repandra** Lindl., *Gen. Sp. Orch. Pl.*, 349 (1838); Linder, *Contr. Bolus Herb.*, **9**, 70 (1981*c*); Stewart *et al.*, *Wild Orch. S. Afr.*, 128 (1982); Linder and Kurzweil, *Orch. S. Afr.*, 210 (1999). Type species: *D. cornuta* (L.) Sw. (lecto.).

The robust plants have cauline, imbricate leaves and dense inflorescences with medium-sized flowers. Petals are falcate and have a prominent basal anticous lobe. A group of three species in southern Africa and ranging into Zimbabwe.

2.4. **Disa** section **Aconitoideae** Kränzl., *Orch. Gen. Sp.*, **1**, 776 (1900); Linder, *Contr. Bolus Herb.*, **9**, 80 (1981*c*); Stewart *et al.*, *Wild Orch. S. Afr.*, 129 (1982); Linder and Kurzweil, *Orch. S. Afr.*, 212 (1999). Type species: *D. aconitoides* Sond.

The group comprises slender plants with cauline leaves, distinctive for the massive spur, the falcate petals, and the extensive fusion of rostellum and petals. The group comprises eight grassland species and is largely tropical.

3. **Disa** subgenus **Hircicornes** (Kränzl.) H.P.Linder, *Contr. Bolus Herb.*, **9**, 105 (1981*c*). Type species: *D. hircicornis* Rchb.f.

Disa section *Hircicornes* Kränzl., *Orch. Gen. Sp.*, 757 (1900).

3.1. **Disa** section **Hircicornes** Kränzl., *Orch. Gen. Sp.*, **1**, 757 (1900); Linder, *Contr. Bolus Herb.*, **9**, 105 (1981*c*); Stewart *et al.*, *Wild Orch. S. Afr.*, 118 (1982); Linder and Kurzweil, *Orch. S. Afr.*, 214 (1999). Type species: *D. hircicornis* Rchb.f. (lecto.).

A large group of robust plants with sterile shoots and flowers with an elliptic to spathulate lip and elongate spur. The 16 species are found in montane grassland in southern and central Africa and Madagascar.

3.2. **Disa** section **Monadenia** (Lindl.) Bolus, *Trans. S. Afr. Phil. Soc.*, **5**, 137 (1888); Linder and Kurzweil, *Orch. S. Afr.*, 223 (1999). Type species: *D. brevicornis* (Lindl.) Bolus (lecto.).

Monadenia Lindl., *Gen. Sp. Orch. Pl.*, 356 (1838); Rolfe, *Fl. Cap.*, **5** **(3)**, 186 (1912); Schelpe, *Intro. S. Afr. Orch.*, 82 (1966); Linder, *Bothalia*, **13**, 341 (1981*e*); Stewart *et al.*, *Wild Orch. S. Afr.*, 148 (1982); Linder in la Croix and Cribb, *Fl. Zamb.*, **11**, 197 (1995). Type species: not designated.

Slender herbs with cauline leaves. The flowers are small to minute and are borne in a dense raceme. The most distinctive character of the group is the unlobed or only weakly three-lobed rostellum which normally bears a single viscidium (except in *D. cylindrica* (Thunb.) Sw.). The group of 18 species is mainly found in the western and eastern Cape of South Africa, although one species ranges into KwaZulu-Natal and tropical Africa.

3.3. **Disa** section **Ovalifoliae** H.P.Linder, *Contr. Bolus Herb.*, **9**, 147 (1981*c*); Stewart *et al.*, *Wild Orch. S. Afr.*, 123 (1982); Linder and Kurzweil, *Orch. S. Afr.*, 235 (1999). Type species: *D. ovalifolia* Sond.

Slender plants with cauline leaves and erect petals. The single species is found in the western Cape of South Africa.

3.4. **Disa** section **Stoloniferae** H.P.Linder, *Contr. Bolus Herb.*, **9**, 150 (1981*c*). Type species: *D. stairsii* Kränzl.

Plants spreading with stolons, tubers apparently absent. Two species in swamps and high-elevation rainforests in central and eastern Africa.

4. **Disa** subgenus **Stenocarpa** (Lindl.) H.P.Linder, *Contr. Bolus Herb.*, **9**, 155 (1981*c*). Type species: *D. porrecta* Sw.

Disa sect. *Stenocarpa* Lindl., *Gen. Sp. Orch. Pl.*, 352 (1838).

4.1. **Disa** section **Amphigena** Bolus, *Trans. S. Afr. Phil. Soc.*, **5**, 139 (1888); Linder, *Contr. Bolus Herb.*, **9**, 156 (1981*c*); Stewart *et al.*, *Wild Orch. S. Afr.*, 114 (1982); Linder and Kurzweil, *Orch. S. Afr.*, 235 (1999). Type species: *D. tenuis* Lindl.

Slender grass-like herbs, leaves radical and often hysteranthous. The small flowers are variable, particularly in the spur length, and are subtended by bracts which are dry at flowering time. Four species in the Cape floristic region belong to this group.

4.2. **Disa** section **Coryphaea** Lindl., *Gen. Sp. Orch. Pl.*, 350 (1838); Linder, *Contr. Bolus Herb.*, **9**, 165 (1981*c*); Stewart *et al.*, *Wild Orch. S. Afr.*, 115 (1982); Linder and Kurzweil, *Orch. S. Afr.*, 238 (1999). Type species: *D. sagittalis* (L.f.) Sw. (lecto.).

Slender to robust plants with basal or cauline leaves. A heterogeneous section, with two morphologically distinct groups. Nine species are placed here. Eight are largely restricted to the Cape floristic region, and one is endemic to the island of Réunion.

4.3. **Disa** section **Stenocarpa** Lindl., *Gen. Sp. Orch. Pl.*, 352 (1838); Linder, *Contr. Bolus Herb.*, **9**, 189 (1981*c*); Stewart *et al.*, *Wild Orch. S. Afr.*, 105 (1982); Linder and Kurzweil, *Orch. S. Afr.*, 243 (1999). Type species: *D. gladioliflora* Burch. ex Lindl.

Slender to robust herbs with firm leaves which are either fresh and cauline, or hysteranthous and basal. Inflorescences are usually capitate. The dorsal sepal has a long spur generally at least as long as the lateral sepals. The section may not be distinct from sect. *Herschelianthe*. Fifteen species in southern and central Africa.

4.4. **Disa** section **Herschelianthe** (Rauschert) H.P.Linder, Linder & Kurzweil, *Orch. S. Afr.*, 255 (1999). Type species: *D. graminifolia* Ker-Gawl. ex Spreng.

Herschelia Lindl., *Gen. Sp. Orch. Pl.*, 362 (1838); Rolfe, *Fl. Cap.*, **5** (3), 199 (1913); Schelpe, *Intro. S. Afr. Orch.*, 86 (1966); Linder, *Contr. Bolus Herb.*, **9**, 368 (1981*c*); Stewart *et al.*, *Wild Orch. S. Afr.*, 143 (1982).

Non *Herschellia* Bowdich, Bot., Excurs. Madeira Pto. Santo, 159 (1825).

Herschelianthe Rauschert, *Feddes Repert.*, **94**, 434 (1983); Linder in la Croix and Cribb, *Fl. Zamb.*, **11**, 194 (1995).

Slender, grass-like herbs with hysteranthous leaves and lax, few-flowered inflorescences. Flowers often blue and generally with falcate petals; lip ovate and frequently fringed. Sixteen species in southern and south-central Africa

4.5. **Disa** section **Emarginatae** H.P.Linder, *Contr. Bolus Herb.*, **9**, 240 (1981*c*); Stewart *et al.*, *Wild Orch. S. Afr.*, 112 (1982); Linder and Kurzweil, *Orch. S. Afr.*, 266 (1999). Type species: *D. stachyoides* Rchb.f.

Slender plants with cauline leaves. The dorsal sepal is shallowly galeate and has a spur that is horizontal at the base. A distinct feature is the rostellum which has a large finger-like central lobe. Five species of this group are widespread in the southern African summer-rainfall region, and one is endemic to Madagascar.

4.6. **Disa** section **Austroalpinae** H.P.Linder, *Contr. Bolus Herb.*, **9**, 263 (1981*c*); Stewart *et al.*, *Wild Orch. S. Afr.*, 104 (1982); Linder and Kurzweil, *Orch. S. Afr.*, **270** (1999). Type species: *D. basutorum* Schltr.

Slender plants with flowers with ascending spur and square petals. A small group of three species in high-elevation grasslands of southern, central, and eastern Africa.

5. **Disa** subgenus **Disa**

5.1. **Disa** section **Disa**, H.P.Linder, *Contr. Bolus Herb.*, **9**, 270 (1981*c*); Stewart *et al.*, *Wild Orch. S. Afr.*, 130 (1982); Linder and Kurzweil, *Orch. S. Afr.*, 271 (1999). Type species: *D. uniflora* Bergius.

Plants slender to fairly robust, with basal or cauline leaves. Flowers resupinate or not, medium-sized or large, borne in corymbose or racemose inflorescences. Spur short or absent; petals reflexed. A large group of 22 species in the western Cape of South Africa, with one species extending into KwaZulu-Natal. Most species grow associated with water or fairly wet habitats.

5.2. **Disa** section **Phlebidia** Lindl., *Gen. Sp. Orch. Pl.*, 350 (1838); Linder, *Contr. Bolus Herb.*, **9**, 328 (1981*c*); Stewart *et al.*, *Wild Orch. S. Afr.*, 139 (1982); Linder and Kurzweil, *Orch. S. Afr.*, 287 (1999). Type species: *D. longicornu* L.f.

Slender plants with basal leaves and a single blue or white flower which has reflexed petals. Three species in crevices on wet cliffs in the western Cape of South Africa. **(HK, PL)**

Phylogenetics

In the past, a few groups within *Disa* have been recognized as distinct genera (*Amphigena*, *Orthopenthea*, *Penthea*, *Herschelia*, *Monadenia*). Of these, only *Disa*, *Herschelia*, and *Monadenia* were upheld in the recent revisions of Linder (1981*b*, *c*, *d*, *e*, *f*). *Herschelia* later had to be renamed as *Herschelianthe* (Rauschert 1983). Johnson *et al.* (1998*a*), in a phylogenetic analysis based on morphological data, stressed that *Herschelianthe* was the sister group of *Disa* sect. *Stenocarpa* and that *Monadenia* was sister to *D.* sect. *Hircicornes*. Douzery *et al.* (1999), using ITS sequence data but with a much smaller sample of species, corroborated the nesting of both *Herschelianthe* and *Monadenia* in *Disa*, but placed both as sisters to *D.* sect. *Micranthae*.

Following Lindley (1838) attempts were made to subdivide the large genus *Disa* into sections, although this was not always intended to reflect phylogenetic relationships. In a recent revision of *Disa* (Linder 1981*c*, *d*; excluding the sections *Monadenia* and *Herschelianthe*) 15 sections were recognized. The sections were separated by morphological and particularly floral morphological characters. These include leaf shape and position, spur shape and orientation, and degree of fusion of the rostellum to the petals. Attempts to resolve the phylogenetic relationships among the sections (Linder 1986*a*; Linder and Kurzweil 1994) were unsuccessful. Further research is needed here. **(HK, PL)**

Ecology

Disa is the largest genus within Diseae and expectedly diverse in its habitat preferences. Whereas most species are found in natural vegetation, a few favour man-made habitats such as road-cuts (*D. woodii* Schltr., *D. chrysostachya*) or pine plantings (*D. bracteata* Sw.). Most *Disa* species occur in damp or wet habitats. In contrast, dry areas are almost free of *Disa* species (one of the few exceptions is *D. karooica* S. D. Johnson & H. P. Linder). Habitats of *Disa* species in the Cape floristic region range from the coastal sand plain (*D. cornuta*, *D. draconis* Sw., several species of *D.* sect. *Monadenia*) to high-elevation fynbos (*D. harveiana* Lindl., many species of *D.* sects. *Disella* and *Disa*). Some *Disa* species grow next to running water or below waterfalls (*D. uniflora*, *D. cardinalis* H.P.Linder, *D. caulescens* Lindl., *D. tripetaloides* N.E.Br., *D. uncinata* Bolus), whereas others make up a large part of the rock-flush vegetation (*D. richardiana* Lehm. ex Lindl., *D. rosea* Lindl., *D. telipogonis* Rchb.f., species of *D.* sect. *Phlebidia*). Others such as *D. pillansii* L.Bolus prefer mountain marshes. Many *Disa* species occur in the grasslands of the southern and south-central African summer-rainfall area, both in lowland (especially if this is seasonally wet; e.g. *D. caffra* Bolus), and grassland in the middle elevations (*D. cornuta*, *D. erubescens* Rendle, *D. perplexa* H. P. Linder, *D. aconitoides*, several species of *D.* sect. *Stenocarpa* and *Hircicornes*). Few *Disa* species are found in grassland at very high elevations, examples are *D. fragrans* Schltr. and *D. basutorum*. In central Africa many *Disa* species can be found in seasonal marshes (dambos) as well as in savanna woodland. The eastern African *D. stairsii* is found in either high-elevation rainforest or in marshy alpine grassland. Most tropical species occur in montane grassland (e.g. *D. baurii* Bolus and its allies, *D. ochrostachya* Rchb.f.). Fewer species are found in *Brachystegia* woodland (e.g. *D. walleri* Rchb.f.).

Some species, particularly in the western Cape of South Africa, are dependent on previous burning of their habitat. In most species the flowering is clearly enhanced by veld fires, and a sudden mass-flowering can often be seen in a recently burnt area. A number of species seem to flower exclusively after a fire, i.e. they require the stimulus brought by the burning (e.g. *D. introrsa* H.Kurzweil, W.R.Liltved & H.P.Linder, *D. micropetala* Schltr., *D. subtenuicornis* H.P.Linder, *D. atrorubens* Schltr., *D. bodkinii* Bolus, *D. begleyi* L. Bolus). Flowering individuals can usually only be found in the first year after the fire. In several species, however, flowering does not seem to be affected by fire (stream-side and rock-flush species, *D. graminifolia* Ker-Gawl. ex Spreng., *D. purpurascens* Bolus, *D. cornuta*, *D. sagittalis*, *D. tenella* (L.f.) Sw., *D. ferruginea* (Thunb.) Sw.).

Flowering of most species in the South African winter-rainfall area occurs in spring, with high-elevation and stream-side species flowering in late spring to early summer. Hysteranthous species of the South African winter-rainfall area can be seen flowering in late summer and autumn. Also, the species of the African summer-rainfall region flower during or after the rains, i.e. in summer or early autumn.

The soil where *Disa* species are found may be deep or shallow, and several species grow in rock crevices with very small amounts of substrate (e.g. *D. telipogonis*, *D. rosea*, *D. maculata* L.f., *D. longicornu*). Soils are usually fairly nutrient-poor in the Cape floristic region. They can be made up of sand or rock derived from Table Mountain sandstone, or peat-like and rich in organic matter. *Disa* species are rare on the richer soils derived from shales; these are usually the habitats of *Disperis*, *Pterygodium*, and *Corycium*.

Although a number of species always grow solitarily or scattered in groups of three to five specimens (the best example is *D. cornuta*), others grow in large but widely scattered populations (e.g. *D. ferruginea*, *D. graminifolia*, *D. purpurascens*). Many other species can form dense and extensive colonies of hundreds of individuals nearly growing side by side (e.g. *D. tenella*, *D. sagittalis*, *D. cooperi* Rchb.f., *D. obtusa* Lindl., *D. bivalvata* (L.f.) Dur. & Schinz, *D. comosa* (Rchb.f.) Schltr., *D. bolusiana* Schltr.). Some species are hardly ever seen in flower because they are very local in their distribution range (e.g. *D. subtenuicornis* H.P.Linder, *D. introrsa*, *D. maculomarronina* D. McMurtry, *D. clavicornis* H.P.Linder, *D. macrostachya* (Lindl.) Bolus, *D. cochlearis* S.D.Johnson & W. R. Liltved, *D. arida* Vlok, *D. newdigateae* L. Bolus, *D. schlechteriana* Bolus, *D. intermedia* H. P. Linder, *D. begleyi*, and *D. aurata* (Bolus) L.Parker & H.Koopowitz), and many other species are thought to be rare because of their sporadic appearance in response to fire. However, a few species appear to be genuinely rare, and only very few plants are found in their area of occurrence at the right time and in the right habitat. The frequent occurrence of such genuinely rare species in *D.* sect. *Disella* was pointed out by Linder (1990). **(HK, PL)**

Pollination

Disa ranks among the most diverse of all terrestrial orchid genera. Johnson *et al.* (1998*a*) have shown that adaptive radiation in *Disa* has been closely associated with the evolution of a remarkable array of pollination systems (Figs 14.4, 14.5). By contrast, flowers of many other orchid genera are pollinated largely by a single group of insects, e.g. *Catasetum* pollinated by euglossine bees (Dressler 1993), *Disperis* pollinated by oil-collecting bees (Steiner 1989; Manning and Linder 1992), and *Angraecum* pollinated mainly by moths (c.f. Dressler 1993).

The median (dorsal) sepal in *Disa* is usually galeate and modified to form a spur, and the column is situated below the entrance to the floral chamber. Consequently, pollinaria placement is sternotrobic, on the underside of the pollinators, either on the proboscis, legs, or ventral surface of the thorax. Most Orchideae, by contrast, are characterized by nototrobic placement of pollinaria.

The celebrated discovery of how *D. uniflora* is pollinated by the mountain pride butterfly, *Meneris tulbaghia* (Nymphalidae; Satyrinae), was made by Marloth (1896). The complex floral mechanism of *D. uniflora* has been described by Trimen (1864) and is only briefly summarized here. Nectar is produced in a spur protruding from the rear of the dorsal sepal. A butterfly alighting on the flower usually straddles the rostellum lobes with its legs while inserting its proboscis into the spur (Fig. 14.5D). The viscidia adhere to the legs of the butterfly, and, when the next flower is visited, the elongated pollinaria dangle onto the stigma directly below the rostellum. Plants of *D. uniflora* growing in steep-sided gorge habitats produce more fruits than their counterparts growing in open valleys as the mountain pride butterfly prefers rocky habitats (Johnson and Bond 1992). Remarkably, this is the only butterfly species known to visit and pollinate the spectacular red flowers of this species. Johnson and Bond (1994) showed that the mountain pride butterfly has an exclusive preference for red/orange flowers and is the sole pollinator of a guild of about 20 South African plant species.

The mountain pride butterfly also pollinates the non-rewarding flowers of *D. ferruginea* (Marloth 1896). Johnson (1994*a*) showed

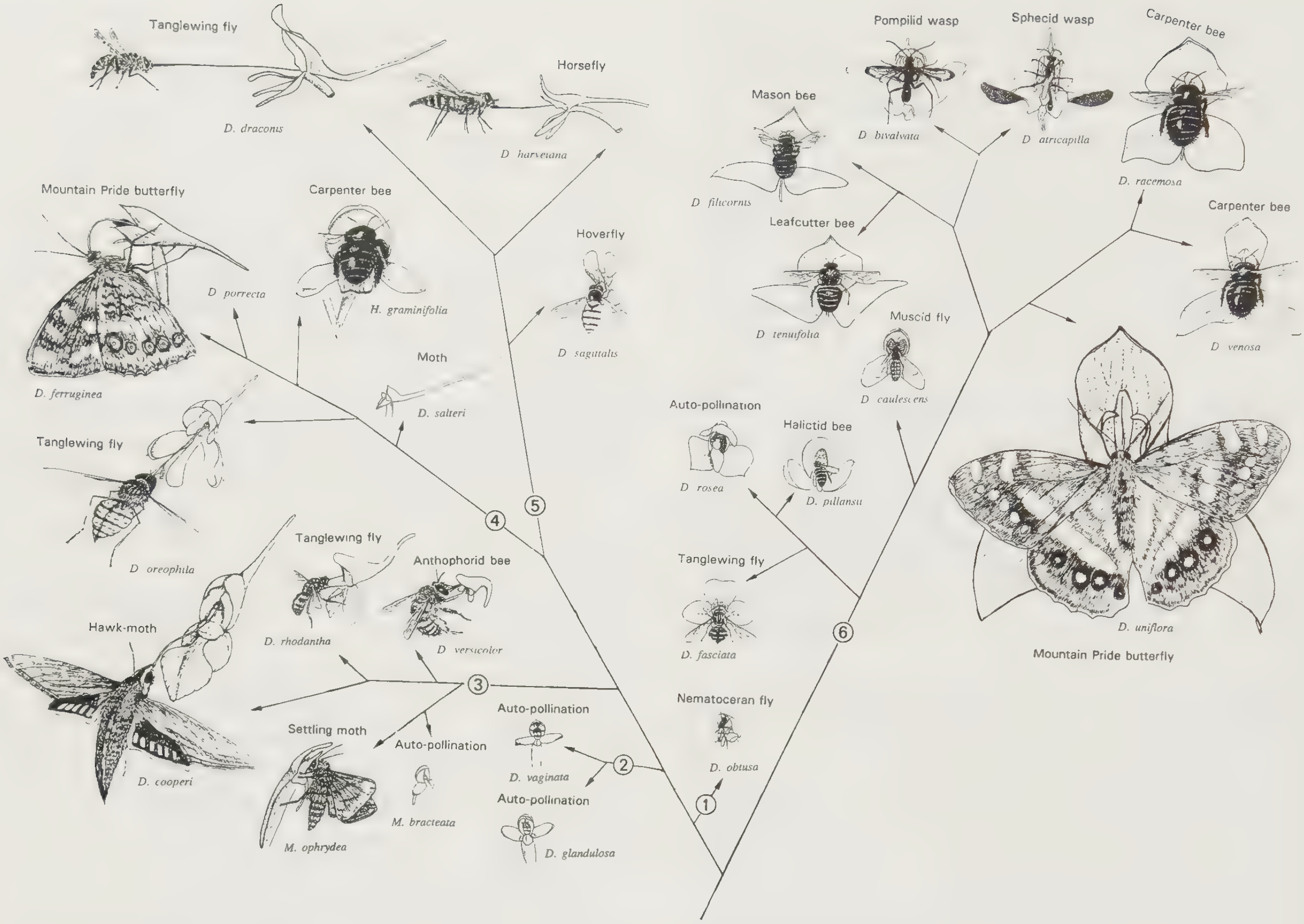

Fig. 14.4. The evolutionary radiation of some pollination systems in *Disa*, based on a phylogeny of the genus (after Johnson *et al.* 1998*a*).

that *D. ferruginea* is a Batesian mimic; butterflies are attracted to its flowers because of their resemblance to sympatric nectar-producing flowers. Interestingly, there are two colour morphs of *D. ferruginea.* In the western Cape, a red form of *D. ferruginea* imitates the red flowers of *Tritoniopsis triticea* (Burm. f.) P. Goldblatt, whereas in the southern Cape an orange form imitates the orange flowers of *Kniphofia uvaria* (L.) Oken. Butterflies that have visited the rewarding flowers of the model species are more likely to visit (mistakenly) the orchid. Consequently, *D. ferruginea* has higher levels of pollination success where it grows in sympatry with one of its models, *T. triticea*, than in places where it grows alone.

Pollination by moths is not as common in *Disa* as it is in *Satyrium* and the various epiphytic genera in Africa. Members of *Disa* section *Monadenia* mostly produce nectar in a long spur and have evening-scented flowers that attract moths (Fig. 14.5F). The flowers have a single viscidium. In *D. ophrydea* Bolus the pollinaria are attached ventrally to the base of the moth's proboscis (Johnson 1995*a*). *Disa ophrydea* has dark beetroot-red flowers, quite unlike typical moth-pollinated flowers, which are white. Terrestrial orchids are often severely grazed by antelope and hyraxes in the Cape region. Johnson (1995*a*) suggested that the dark colour of flowers of *D. ophrydea* renders them cryptic to herbivores in the blackened post-fire environment.

Pollination by hawkmoths has been reported in the grassland species *Disa cooperi*, a member of section *Hircicornes* (Johnson 1995*b*) (Fig. 14.5B). The broad scent-producing lip is an autapomorphic feature in *D. cooperi*, indicating that moth-pollination is recently derived in this clade, possibly from a long-tongued, fly-pollinated ancestor. Only hawkmoths with tongues shorter than the spur (*c.* 40 mm) are effective pollinators; moths with longer tongues, such as *Agrius convolvuli*, act as nectar robbers. The petals play an important role in 'channelling' the proboscis over the rostellum lobes, which bear two closely adjacent viscidia. When fully inserted, pollinaria are attached to the ventral base of the proboscis (Fig. 14.5A).

Bee pollination has evolved at least five times in *Disa* (Johnson *et al.* 1998*a*). The floral spur of *D. versicolor* Rchb.f. is nectariferous and sharply decurved, matching the long curved tongue of *Amegilla natalensis*, an anthophorid bee species that pollinates this orchid at several sites in the Drakensberg (Johnson 1994*b*; Fig. 14.5C). The flowers change colour from pink to brown during anthesis, perhaps a cue for bees to find receptive flowers on the elongated inflorescence.

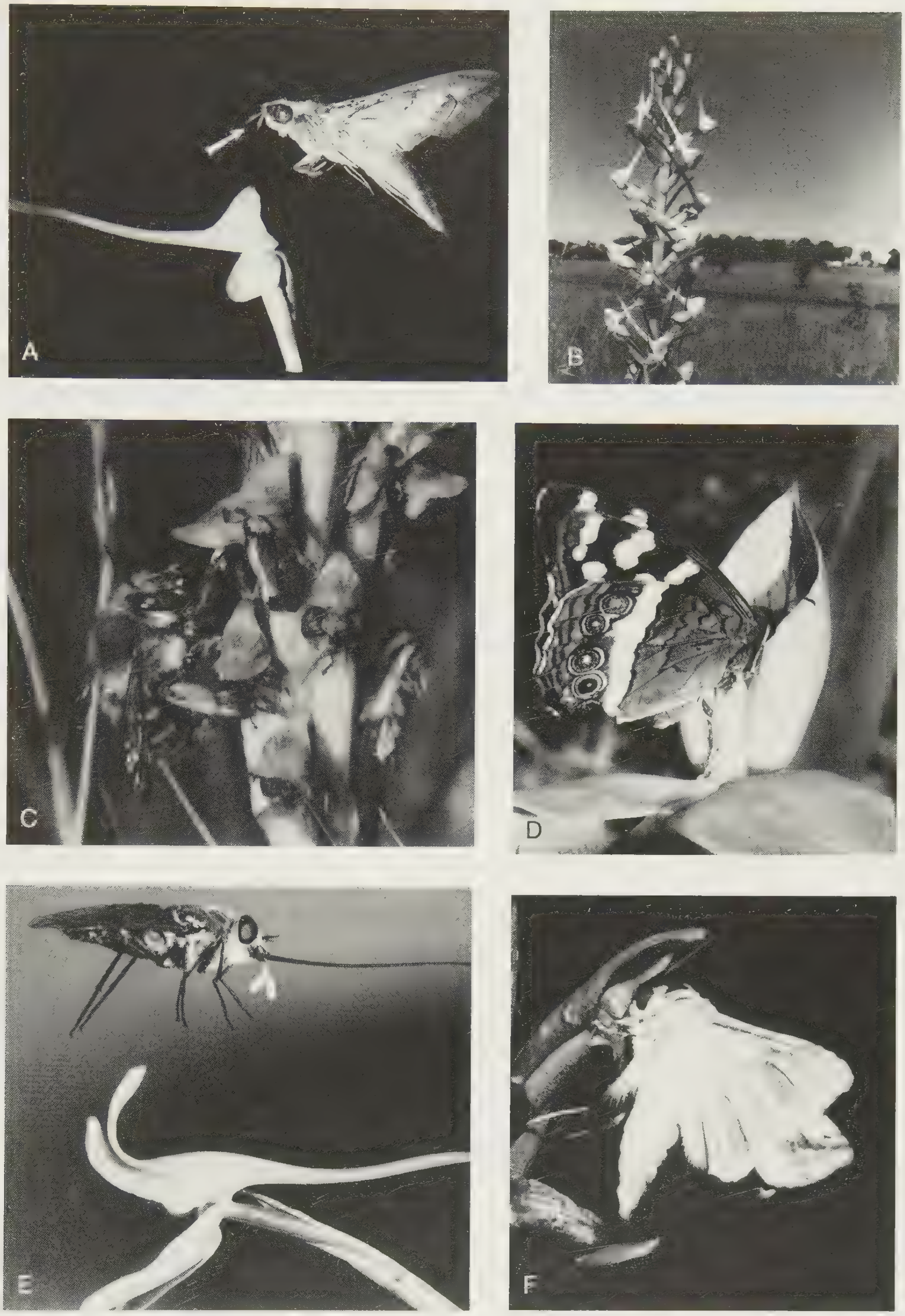

Fig. 14.5. Flowers and pollinators of *Disa* species. A. Hawkmoth *Basiothia schenki* posed next to a flower of *Disa cooperi*. Pollinaria on the tongue are arrowed. B. Inflorescence of *Disa cooperi*. C. Anthophorid bee *Amegilla natalensis* visiting flowers of *Disa versicolor*. D. Mountain Pride butterfly (*Meneris tulbaghia*) feeding on nectar of *Disa uniflora*. Pollinaria are attached to the legs of the butterfly. E. Long-tongued fly (*Philoliche rostrata*), posed next to a flower of *Disa harveiana*. Pollinaria are attached to the proboscis of the fly. F. A noctuid moth (*Syngrapha circumflexa*) with its proboscis fully inserted into the nectariferous spur of *Disa ophrydea* (after Johnson 1994*b*, 1995*a, b*; Johnson and Bond 1994; Johnson and Steiner 1997).

Bumblebees (*Bombus* spp.) are absent from southern Africa; their ecological role as pollinators of large complex flowers is instead carried out by carpenter bees belonging to the genus *Xylocopa*. Carpenter bees have been shown to be responsible for the pollination of several *Disa* species. The pollination of the blue disa, *D. graminifolia*, was an unsolved mystery until recently when it was shown that carpenter bees visit and pollinate its flowers (Johnson 1993*b*). *Disa graminfolia* is a deceptive species, relying on a generalized resemblance to food plants. The sky-blue flowers are produced during autumn, a trough in the flowering season when carpenter bees explore possible new food sources. The pollinaria are attached to the underside of the bee's thorax by means of a single large viscidium. Previous attempts by Marloth to observe pollinators of *D. graminifolia* were probably thwarted by the brief and infrequent nature of the visits.

Carpenter bees also pollinate the large pink non-rewarding flowers of *Disa racemosa* and its similar sister species *D. venosa*. Most of the bees found carrying pollinaria of *D. racemosa* were female, prompting Johnson *et al.* (1998*b*) to suggest that the orchid deceives mainly pollen-seeking insects, as male bees do not collect pollen. The floral mechanism of *D. racemosa* ensures that pollinaria are placed precisely on the middle pair of legs. The floral morphology of *D. venosa* is virtually identical, and the two species co-occur at many sites and appear to share pollinators. The absence of hybrids between these two species seems to be the result of a genetic barrier to hybridization, as none of the experimental crosses between these two species yielded viable seed (Johnson *et al.* 1998*b*).

Deception of nectar-seeking insects also occurs in *D. filicornis* Thunb. and *D. tenuifolia*, which attract bees belonging to the family Megachilidae (Johnson 1992*a,b*; Johnson and Steiner 1994*b*). An added dimension to the pollination system of *D. tenuifolia* is the tendency of male carder bees to use patches of the bright yellow flowers of this orchid as territorial patrol sites. Vogel (1972) observed similar patrolling behaviour in male *Eucera* bees that pollinate *Anacamptis* (= *Orchis*) *papilionacea* R.M. Bateman, Pridgeon & M.W. Chase. Bees settle momentarily on the flowers of *D. tenuifolia* during territorial flights, and highly elongated pollinaria (*c.* 10 mm in length) are attached to the underside of the thorax when they contact the hornlike rostellum lobes projecting above the flower. Male carder bees patrol areas likely to be frequented by female bees. Johnson and Steiner (1994*b*) speculated that a general resemblance between the flowers of *D. tenuifolia* and the yellow legume flowers frequented by female carder bees may induce male bees to patrol the orchid populations.

The first example of sexual deception in southern African orchids was reported by Steiner *et al.* (1994). *Disa atricapilla* Bolus and *D. bivalvata* Druce are pollinated by male sphecid and pompiliid wasps, respectively. These two species co-occur and flower at the same time, but hybrids are rare owing to the specificity of the wasp pollinators. Occasional breakdown in species integrity was attributed to indiscriminate visits by hopliinid beetles. Although the two orchid species are visited almost exclusively by male wasps, copulatory behaviour has not been observed, indicating that the development of this form of deception is not as advanced in *Disa* as it is in many European and Australian orchids.

The small pungent flowers of *D. obtusa* Lindl. are pollinated by bibionid flies (Nematocera: Bibionidae), which are related to mosquitoes (Johnson and Steiner 1994*a*). Although small flies are generally considered to be inefficient pollinators, their sheer abundance translates into high levels of pollination and fruit success for *D. obtusa* (Johnson and Steiner 1994*a*). The sexes of bibionid flies are highly dimorphic; as a consequence, pollinaria generally adhere to the swollen front legs of the female and to the ventral surface of the thorax of the male flies. The flies use the inflorescences as a convenient place to mate but also visit many other plant species; they cannot be considered to depend solely on the orchids, which flower only after infrequent fires.

The flowers of many *Disa* species are splendidly adapted for pollination by long-tongued flies belonging to the families Tabanidae and Nemestrinidae. These large insects, approximately the size of bees, have evolved elongated nectar-feeding proboscides varying from 10–80 mm. *Disa* species pollinated by long-tongued flies have equally long floral spurs to accommodate these long tongues. Pollination of an orchid by long-tongued flies was first recorded in *D. harveiana* by Johnson and Johnson (1993; Fig. 14.5E), and subsequently documented in *D. oreophila* Bolus subsp. *erecta* H.P.Linder (Johnson and Steiner 1995; Fig. 14.6) and the various members of the *D. draconis* complex (Johnson and Steiner 1997). All of these species lack a floral reward and rely on generalized food deception mimicry to attract long-tongued flies. *Disa harveiana* and *D. draconis* are putative sister taxa differing in floral spur length. Johnson and Steiner (1997) showed that an evolutionary shift has occurred between the short-tongued horseflies that pollinate *D. harveiana* in the mountains and long-tongued tanglewing flies that pollinate *D. draconis* on the lowland sandplains. By artificially shortening the floral spurs at a sandplain site, Johnson and Steiner (1997) were able

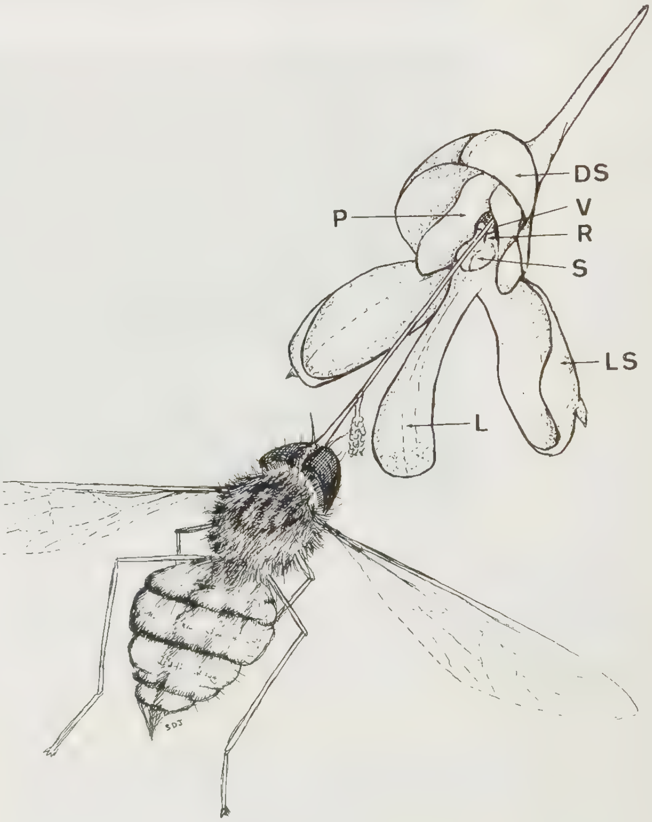

Fig. 14.6. Long-tongued fly (*Prosoeca ganglbauri*) probing a long-spurred flower of *Disa oreophila* subsp. *erecta* (after Johnson and Steiner 1995).

to demonstrate that selection favours longer, rather than shorter, spurs at a site where the pollinator *Moegistorhynchus longirostris* has a long tongue (approximately 60 mm).

Finally, mechanisms of autogamy have evolved at least five times in *Disa*. In section *Micranthae*, autogamy has been reported in *D. erubescens* Rendle (Gassner 1982), *D. ornithantha* Schltr. (Pettersson 1986), and *D. woodii* Schltr. (Johnson 1997*c*). The anther is erect in section *Micranthae*; thus flipping of pollinia onto the stigma is aided by gravity. Johnson (1997*c*) argued that the weedy habit of *D. woodii* (the species frequently colonizes roadsides) is a consequence of autogamy, as seed set is not limited by the paucity of pollinators in disturbed sites. Autogamy has also been implicated in the successful invasion of Australia by the Cape orchid, *D.* (= *Monadenia*) *bracteata* (Kurzweil and Johnson 1993). Autogamy in this species is the result of breakup of pollinia in the anther.

Johnson *et al.* (1994*d*) found that autogamy also occurs in *D. rosea*, *D. vaginata*, and *D. glandulosa*. These three Cape orchids occupy seepage habitats and shady rock clefts high in the Cape mountains which are frequently blanketed in cloud. Unsuitability of these habitats for insect pollinators is probably the main reason for the evolution of autogamy in these species. The caudicle is flexible in all three species, and the pollinia readily flip over onto the stigma when the plants are moved by wind or rain. The viscidia remain functional, so that occasional cross-pollination by insects in these species cannot be ruled out. **(SJ)**

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15. SCHIZODIUM

Schizodium Lindl., *Gen. Sp. Orch. Pl.*, 358 (1838). Type species: *Schizodium flexuosum* (L.) Lindl.

Derivation of name

From the Greek *schizein*, split, and *-odes*, resemblance, referring to the split petals of the species. **(HK, PL)**

Description (Plate 9; Fig. 15.1)

Terrestrial *herbs* with tubers and wiry, flexuose stems. *Leaves* basal and cauline; basal leaves rosette-like, lorate or spathulate; cauline leaves small and lanceolate, base largely sheathing. *Inflorescence* lax, few-flowered. *Flowers* resupinate; ovary often distinct from pedicel. *Dorsal sepal* galeate and spurred, lanceolate; spur straight, curved upward or downward, sometimes basally dorsiventrally constricted. *Lateral sepals* spreading or reflexed, lanceolate to obovate. *Petals* oblong, geniculate, apically bifid, with obscure to prominent basal anticous lobes. *Labellum* pandurate; with concave hypochile; flat, horizontal mesochile; and descending apical unifacial tip. *Column* with horizontal anther; pollinia two, sectile, viscidia globular; stigma cushion-like, shortly stipitate, tripulvinate; rostellum three-lobed with well-developed lateral arms. **(HK, PL)**

Distribution (Fig. 15.2)

Schizodium is endemic to South Africa. The six species are mainly distributed in the western Cape with outliers in the eastern Cape (near Port Elizabeth) and northern Cape (Nieuwoudtville). **(HK, PL)**

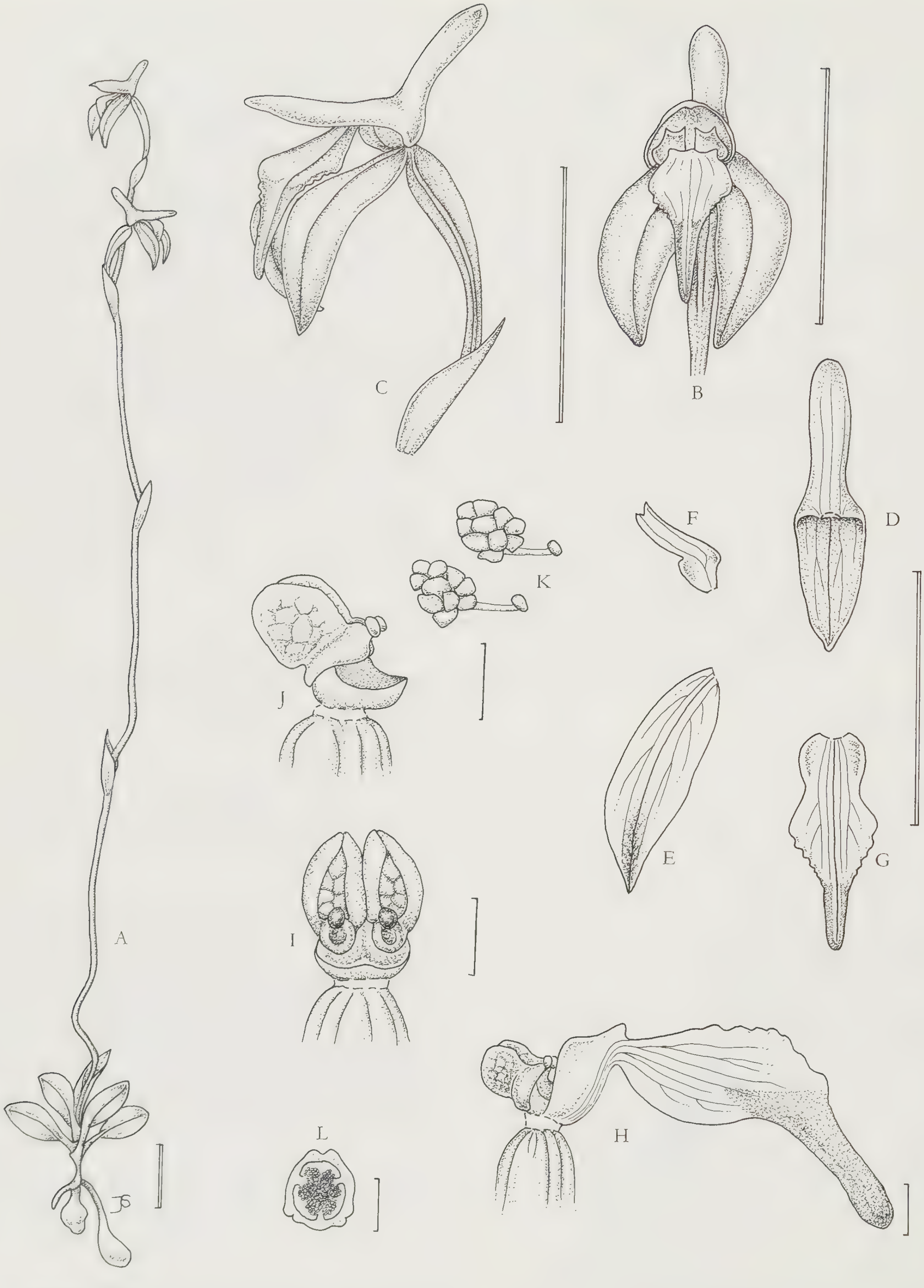

Fig. 15.1. *Schizodium bifidum* (Thunb.) Rchb.f. A. Habit. B. Flower, front view. C. Flower, side view; D. Dorsal sepal; E. Lateral sepal; F. Petal; G. Labellum; H. Labellum, from below, and column, from side; I. Column, front view; J. Column, side view with viscidium nested in rostellum; K. Pollinaria; L. Ovary, transection. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Salter 4724* and Kew Spirit Collection no. 27929.

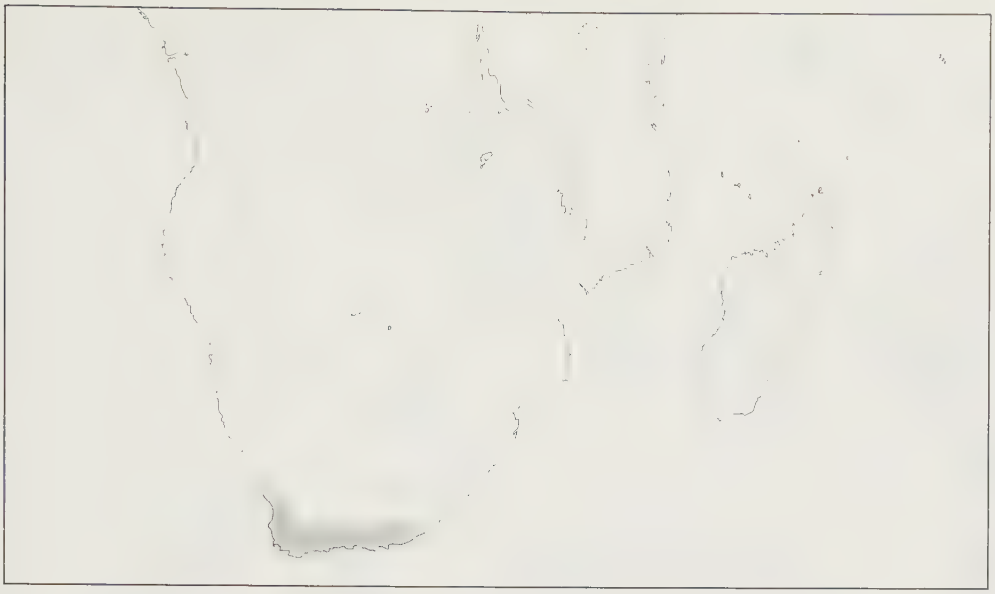

Fig. 15.2. Distribution map of *Schizodium.*

Phylogenetics

Schizodium has been treated as a distinct genus within Disinae by most students of the group (e.g. Lindley 1830–1840; Rolfe 1912–1913; Schelpe 1966; Stewart *et al.* 1982; Linder and Kurzweil 1994). The genus was revised by Linder (1981*b*). Putative synapomorphies of the genus are the pandurate lip and the flexuose, nitid stem (Linder 1986*a*). **(HK, PL)**

Ecology

Schizodium species are found in fynbos, frequently in deep sand derived from Table Mountain sandstone. *Schizodium flexuosum* and *S. obliquum* Lindl. are common in marshy habitats, the latter only in the lowlands, the former over a wide elevation range. *Schizodium bifidum* (Thunb.) Rchb.f. and *S. inflexum* Lindl. occur scattered on well-drained mountain slopes, whereas *S. cornutum* (L.) Schltr. is found on dry coastal sands. *Schizodium longipetalum* Lindl. is a rare species, currently known from a single population in dry fynbos. Flowering has sometimes been recorded after fire, but none of the species is heavily dependent on burning. The species start flowering early in the season, and some plants have been seen in flower as early as June. However, most species flower between August and November. **(HK, PL)**

Pollination

Nothing is known about pollination of *Schizodium.* **(SJ)**

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SUBTRIBE HUTTONAEINAE

Huttonaeinae Schltr., *Notizbl. Bot. Gart. Berlin-Dahlem*, **9**, 568 (1926). Type: *Huttonaea* Harv.

Tribe Huttonaeae (Schltr.) Szlach., *Folia Geobot. Phytotax.*, **26**, 326 (1991).

Description

Glabrous terrestrial *herbs* with root tubers. *Leaves* cauline, lanceolate to ovate, petiolate or sessile. *Inflorescence* a lax terminal raceme. *Flowers* resupinate, one to few. *Sepals* green. *Petals* free or united at the base, clawed and fimbriate, saccate in the upper part, marginally fimbriate. *Labellum* unspurred and unlobed, marginally fimbriate. *Column* without prominent stalk; anther suberect, thecae diverging at the base; pollinia two, sectile; stigma a slightly convex pad on the rostellum; viscidia two. **(HK, PL)**

Distribution (see map for *Huttonaea*)

The subtribe contains only one genus, *Huttonaea*. It occurs from the eastern Cape to Mpumalanga. **(HK, PL)**

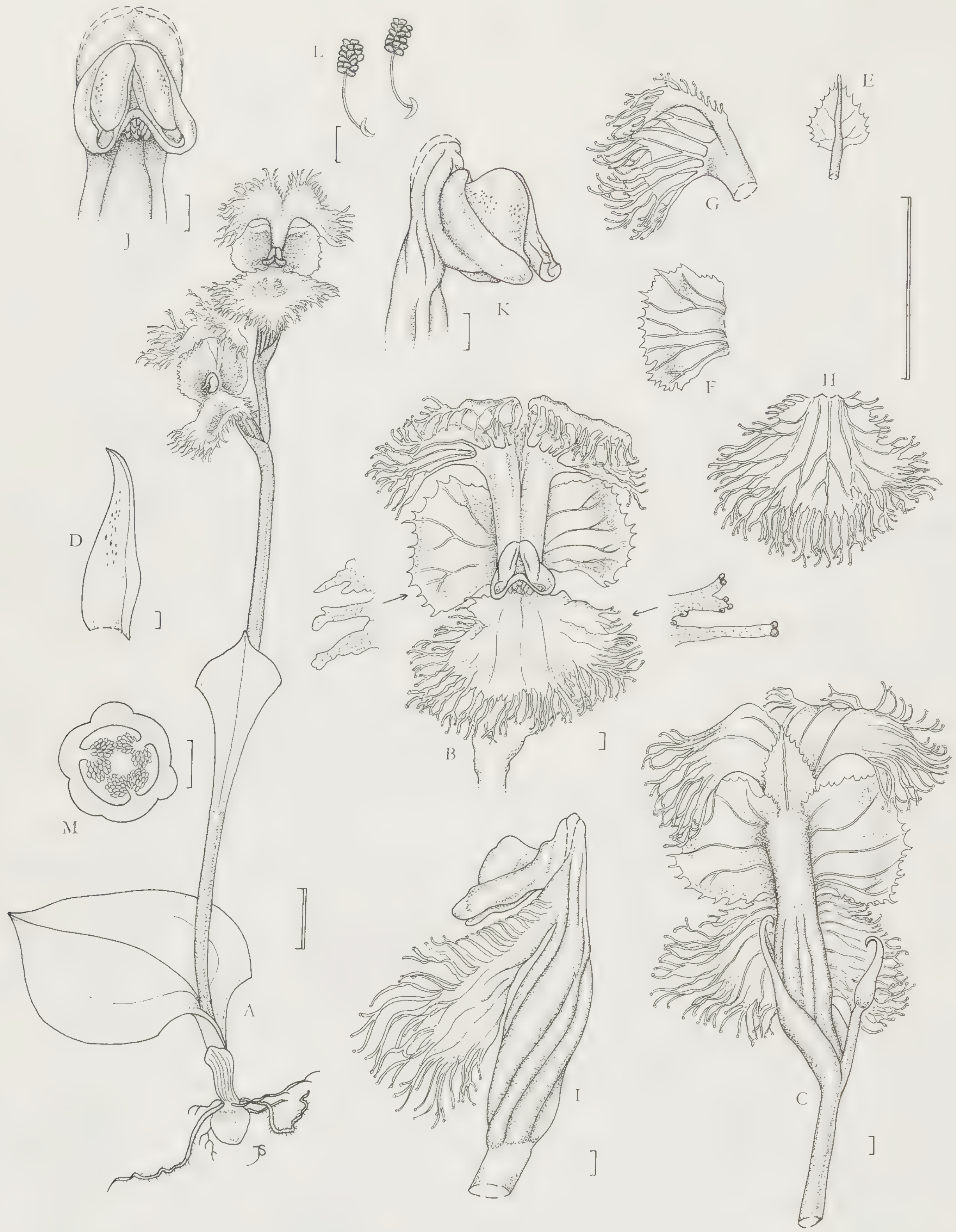

Fig. 16.1. *Huttonaea grandiflora* (Schltr.) Rolfe. A. Habit; B. Flower, front view; C. Flower, back view; D. Bract; E. Dorsal sepal; F. Lateral sepal; G. Petal blade (claw removed); H. Labellum; I. Labellum, column, and ovary, side view; J. Column, front view; K. Column, side view; L. Pollinarium; M. Ovary, transection. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Hilliard &Burt 12551* and Kew Spirit Collection no. 48913.

16. HUTTONAEA

Huttonaea Harv., *Thes. Cap.*, **2**, 1 (1863). Type species: *Huttonaea pulchra* Harv.

Hallackia Harv., *Thes. Cap.*, 2 (1863). Type species: *Hallackia fimbriata* Harv.

Derivation of name

After the plant collectors Henry and Caroline Hutton (19th century), who found the type species, *H. pulchra*, on the Katberg (eastern Cape Province, South Africa). **(HK, PL)**

Description (Plate 10; Fig. 16.1)

Slender terrestrial, tuberous *herbs*, glabrous in all above-ground parts. *Stems* unbranched, up to 40 cm tall, with few leaf sheaths below the leaves. *Foliage leaves* one to few, lower largest, sessile or rarely petiolate, blades elliptic, obtuse to apiculate. *Inflorescence* a lax unbranched raceme, with few flowers; bracts green, lanceolate, as long as ovary. *Flower* resupinate, white to mauve. *Sepals* green, equal or unequal, entire or with serrate margins, lorate to broadly-lanceolate. *Petals* stalked, claws sometimes united with each other and the dorsal sepal, blades saccate and hairy, margins fimbriate. *Labellum* pendent, not spurred, ovate, with lacerate or fimbriate margin. *Column* short, without a prominent stalk; anther with two thecae which are adjacent and parallel or basally diverging; pollinia two, sectile, with two large, separate viscidia; stigma pad-like, positioned on the median stigma lobe. **(HK, PL)**

Distribution (Fig. 16.2)

Five species in the South African summer-rainfall region, from the eastern Cape to Mpumalanga. **(HK, PL)**

Phylogenetics

Huttonaea was previously included in Orchideae (Dressler 1981), but on the basis of the unusual stigma it was placed in Diseae (Linder and Kurzweil 1994). The unusual derivation of the stigma from the median carpel is shared with Coryciinae (Kurzweil 1989, 1991). Because of its peculiar flower structure the genus is considered isolated within Diseae and therefore placed in its own subtribe (Linder and Kurzweil 1994). Further affinities to Diseae include the comparatively simple lip and the large rostellum (Linder 1986*a*).

Preliminary DNA sequence data (Pridgeon and Chase, unpublished) indicate that *Huttonaea* is most closely related to *Pterygodium* and *Corycium* (Coryciinae), but further work is needed to establish its phylogenetic position more firmly.

Ecology

The species of the genus *Huttonaea* are either found in high-elevation grassland (*H. grandiflora*, *H. oreophila* Schltr., *H. woodii* Schltr.) or on the floor of cool montane forests (*H. fimbriata* (Harv.) Rchb.f., *H. pulchra*). The flowering time of the species is fairly late, at the end of summer in March or April. Most of the species are rare but may be locally abundant. **(HK, PL)**

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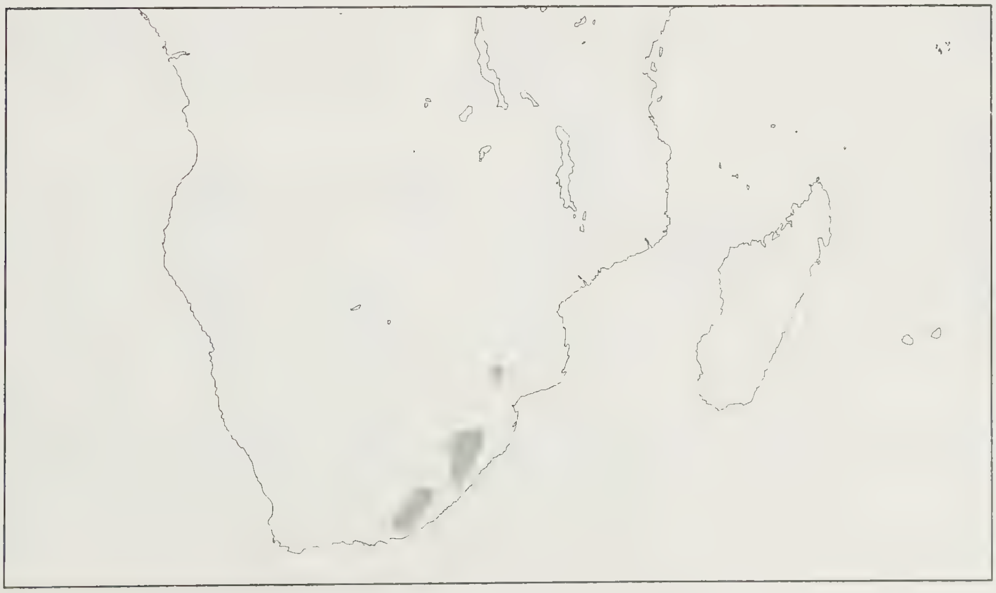

Fig. 16.2. Distribution map of *Huttonaea*.

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SUBTRIBE SATYRIINAE

Satyriinae Schltr., *Notizbl. Bot. Gart. Berlin-Dahlem*, **9**, 568 (1926). Type: *Satyrium* Sw.

Tribe Satyrieae (Schltr.) Szlach., *Folia Geobot. Phytotax.*, **26**, 326 (1991).

Description

Glabrous terrestrial *herbs* with root tubers and slender to stout stems, occasionally with sterile shoots. *Leaves* basal or cauline, linear, lanceolate or ovate, often adpressed to the substrate. *Inflorescence* a terminal spike or raceme, lax or dense, rarely subcapitate. *Flowers* zygomorphic or (possibly secondarily) subactinomorphic, small or medium-sized, non-resupinate. *Sepals* and *petals* similar, petals sometimes marginally fringed. *Labellum* flat-navicular or galeate, usually with elongate or sac-like spurs. *Column* with prominent stalk; anther pendent, normally with fairly elongate thecae, apical connective process rarely present; pollinia two, sectile; stigma usually situated on a flat to navicular flap, rarely pad-like; rostellum mostly developed as a flap, viscidia two or rarely one. **(HK, PL)**

Distribution (see map for *Satyrium,* Fig. 18.3)

The subtribe Satyriinae comprises two genera. *Satyrium* with about 88 species is widespread in Africa and Madagascar and ranges into Asia with two species. *Pachites* with two species is endemic to the western Cape of South Africa. **(HK, PL)**

Phylogenetics

Evidence for the monophyly of *Satyrium* is strong (Kurzweil and Linder 1999). However, the recognition of the genus *Pachites* is mainly based on plesiomorphic characters. The two species are different in details of their flower morphology, indicating that they may not be closely related (Kurzweil 1996). According to Linder and Kurzweil (1994) *Pachites* appears to be a paraphyletic assemblage relative to the remaining members of the Satyriinae clade. **(HK, PL)**

17. PACHITES

Pachites Lindl., *Gen. Sp. Orch. Pl.*, 301 (1835). Type species: *Pachites appressa* Lindl.

Derivation of name

From the Greek *pachys*, thick, and the suffix *-ites*, having the nature of, alluding to the thick column. **(HK, PL)**

Description (Plate 11; Fig. 17.1)

Slender or robust terrestrial *herbs*, with root tubers. *Leaves* 3–12, cauline, narrowly lanceolate or linear, sheathing at the base. *Inflorescence* a terminal, lax or dense raceme, often subcapitate; ovary not twisted. *Flowers* not resupinate. *Sepals* and *petals* subequal, linear to narrowly lanceolate, free. *Labellum* similar, entire or minutely three-lobed, not spurred. *Column* with an elongate undifferentiated stalk; anther pendent, pollinia two, sectile, with two separate viscidia; stigma pad-like and tripulvinate or situated in a cavity under the rostellum; rostellum with two short lobes or three-lobed with large U-shaped central lobe. **(HK, PL)**

Distribution (Fig. 17.2)

The two species of *Pachites* are endemic to the western Cape of South Africa. One species, *P. bodkinii* Bolus, is widespread in the south-western parts of the province, but *P. appressa* is localized in the mountains north-east of Swellendam. **(HK, PL)**

Phylogenetics

Both *Pachites* species have a column with a long undifferentiated stalk, which links them with the other Satyriinae. However, they differ clearly by their subactinomorphic perianth. In the past, *Pachites* has always been recognized as a distinct genus within subtribe Satyriinae on the basis of the subactinomorphic perianth (Lindley 1830–1840; Bentham and Hooker 1883; Pfitzer 1888; Bolus 1889; Kränzlin 1897–1904; Schlechter 1901; Rolfe 1912–1913; Hall 1982; Kurzweil and Linder 1999). Linder (1986*a*) pointed out the possibility that *Pachites* is the 'primitive' form of *Satyrium.* However, the subactinomorphic perianth may also be a secondary condition (Kurzweil 1996), indicating that *Pachites* is fairly advanced. The two *Pachites* species differ considerably in details of their gynostemium morphology, thereby leaving doubt about the monophyly of the genus (Linder and Kurzweil 1994; Kurzweil 1996). **(HK, PL)**

Ecology

The species of this genus grow in comparatively dry, sandy or stony soil in mountain fynbos, and flower exclusively in the first year after a veld fire. Both species are genuinely rare, as they are infrequently seen, even after a fire. *Pachites appressa* is localized in its distribution. However, a veld fire may occasionally result in a sudden mass flowering. Hundreds of flowering individuals of *P. bodkinii*, scattered over a large area, were found after the 1992 fire in Silvermine Nature Reserve near Cape Town. The pollination of the two species is unknown but may be quite interesting because of the subactinomorphic perianth. *Pachites appressa* in particular resembles small-flowered species of other monocots and may well be mimicking such plants. Flowering time is spring. **(HK, PL)**

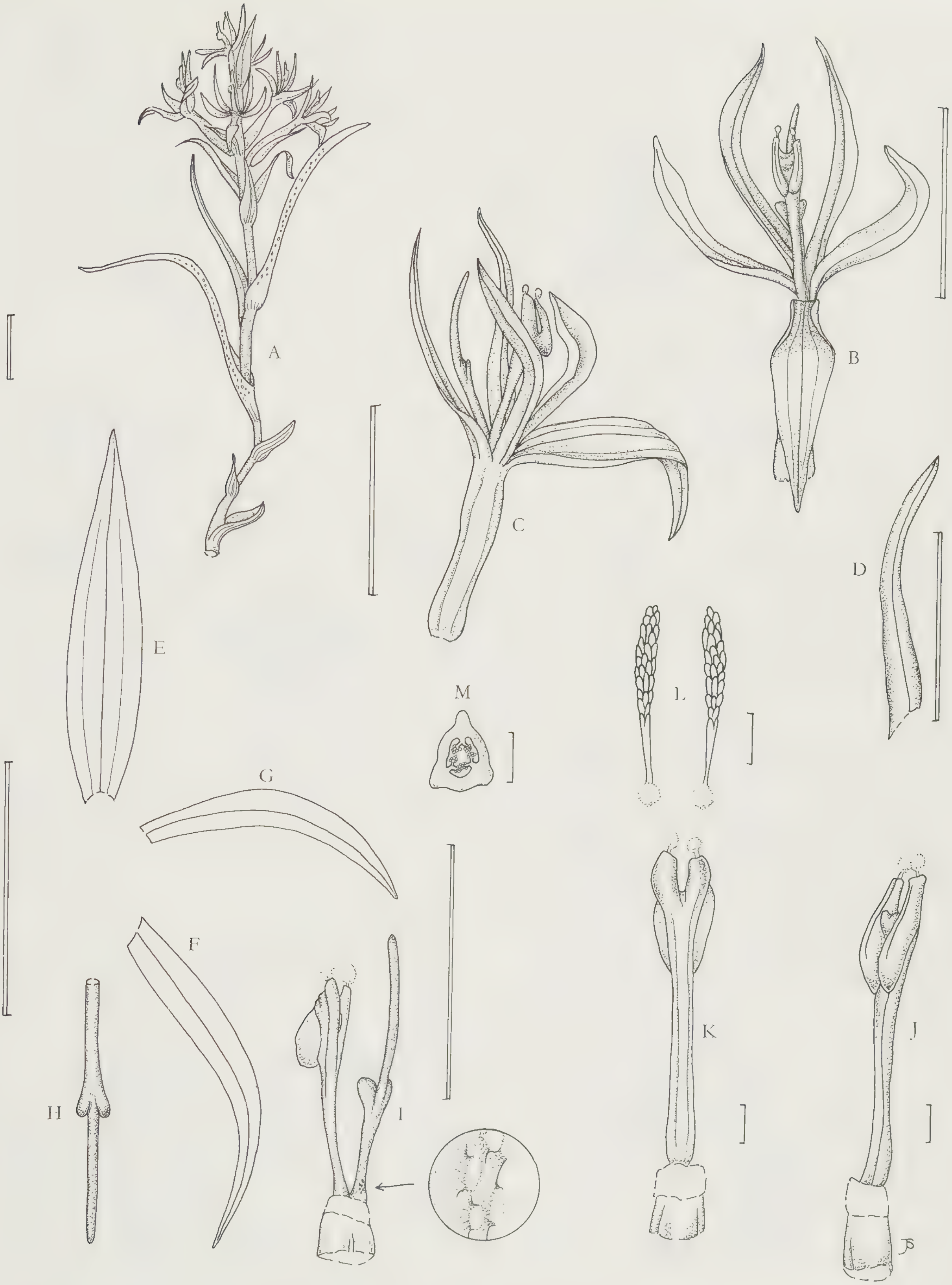

Fig. 17.1. *Pachites bodkinii* Bolus. A. Habit; B. Flower, front view; C. Flower, side view; D. Bract; E. Dorsal sepal; F. Lateral sepal; G. Petal; H. Labellum; I. Labellum and column, side view, inset showing the warts on lower surface of labellum; J. Column, side view; K. Column, back view; L. Pollinaria; M. Ovary, transection. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Schlechter 6970*.

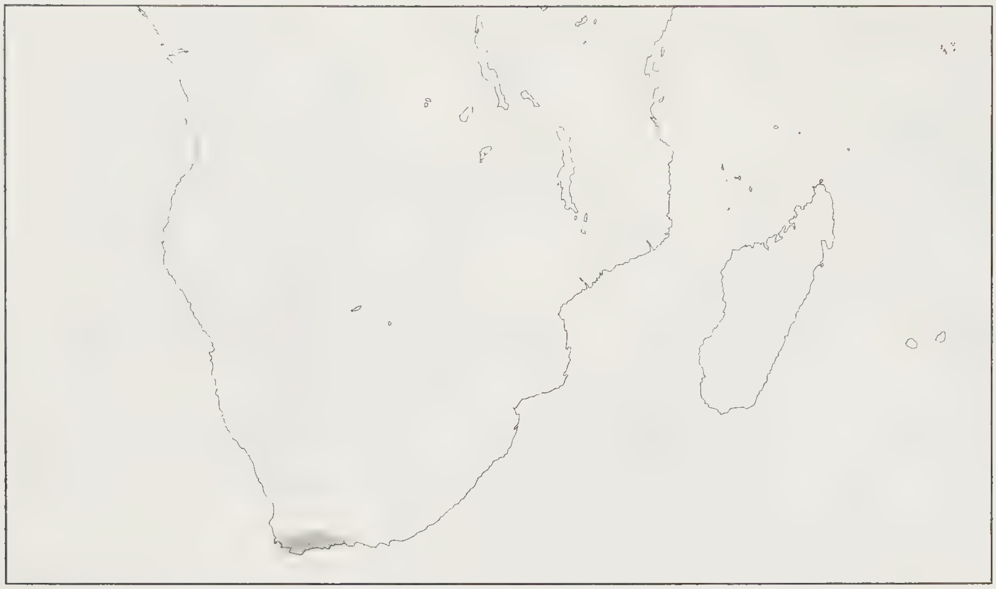

Fig. 17.2. Distribution map of *Pachites.*

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18. SATYRIUM

Satyrium Sw., *Kongl. Vetensk. Acad. Nya Handl.*, ser. **2**, **21**, 214 (1800). Type species: *Satyrium bicorne* (L.) Thunb.

Diplecthrum Pers., *Syn. Pl.*, 508 (1807). Type species: not designated

Hipporkis Thouars, *Nouv. Bull. Sci. Soc. Philom. Paris*, 317 (1809). Type species: not designated

Aviceps Lindl., *Gen. Sp. Orch. Pl.*, 345 (1838). Type species: *Aviceps pumila* (Thunb.) Lindl.

Satyridium Lindl., *Gen. Sp. Orch. Pl.*, 345 (1838). Type species: *Satyridium rostratum* Lindl.

Derivation of name

From the Greek *satyros*, the two-horned satyr, half man-half goat, and the Latin suffix *-ium*, quality or nature of, referring to the two-spurred lip. (**HK, PL)**

Description (Plate 12; Figs 18.1, 18.2)

Slender or robust terrestrial *herbs*, sometimes with sterile shoots that are next year's fertile shoot (Schlechter 1895, 1901), with root tubers. *Tubers* ovoid or elongate, unlobed or rarely bifid, velvety hairy or rarely glabrous, sessile or occasionally stalked. *Roots* few and unbranched, frequently flexuose and hairy. *Stems* unbranched, glabrous, rarely papillose or viscous, with few white or hyaline leaf sheaths below the foliage leaves, upper part of stem above the foliage leaves with sheaths grading into the bracts, sheaths split or tubular. *Foliage leaves* one to few, annual, soft-herbaceous to stiff-fleshy, glabrous, entire, basal or cauline, lanceolate if cauline, ovate to orbicular if basal; basal foliage leaves often flat and adpressed to the ground; in *S. parviflorum* well-developed foliage leaves sometimes absent; leaves green but abaxial surface rarely deep red, normally fresh at flowering time, occasionally withered. *Inflorescence* terminal, lax or dense, with few or many flowers, an elongate raceme or spike, rarely subcapitate; bracts narrowly to broadly lanceolate, acute, glabrous or sometimes ciliate, mostly reflexed from a short ascending base, sometimes erect or spreading, somewhat longer than the ovaries, rarely the lower ones up to ten times

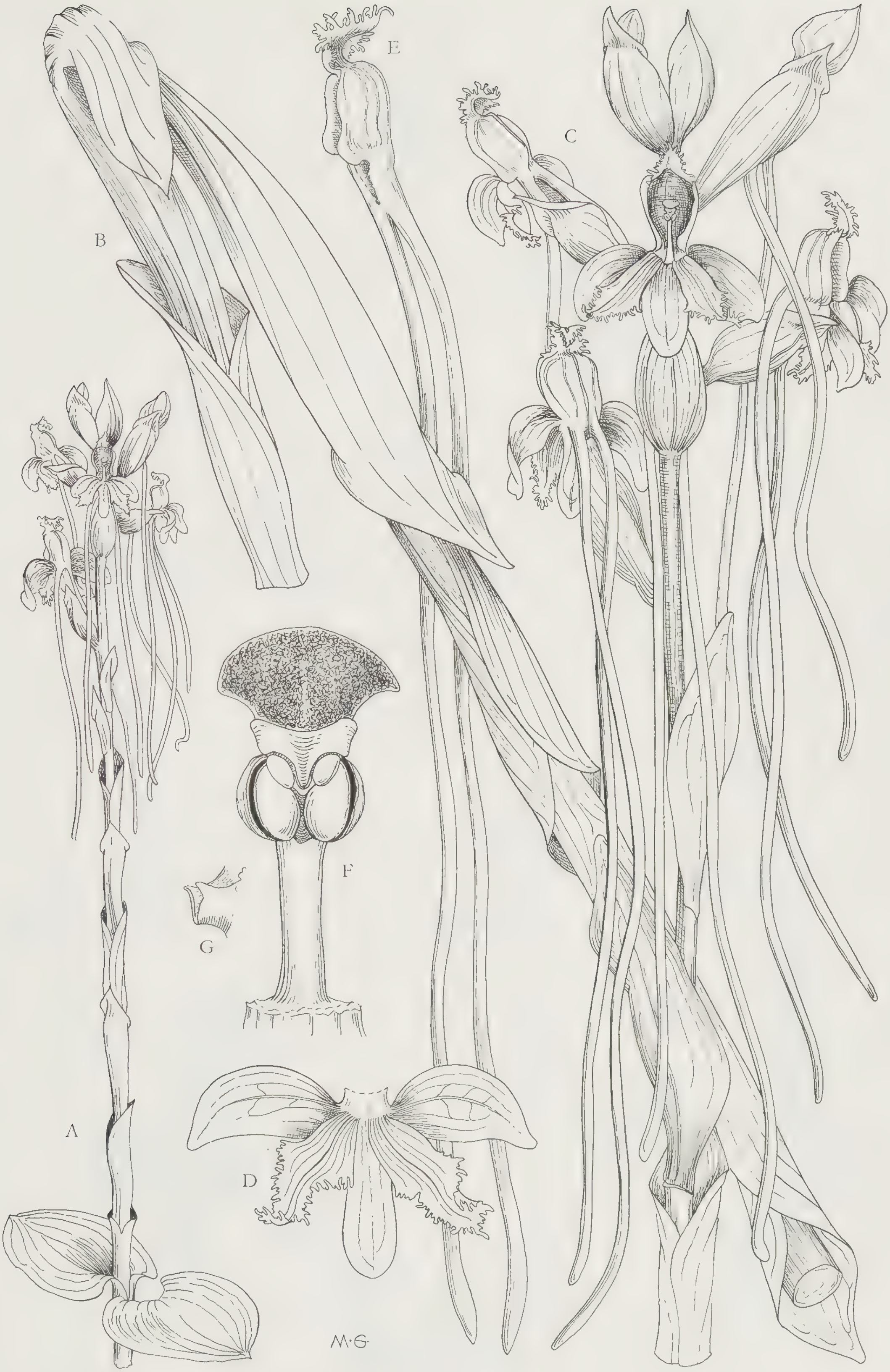

Fig. 18.1. *Satyrium mirum* Summerh. A. Habit, ×0.3; B. Stem, centre portion, ×1; C. Inflorescence, ×1; D. Sepals and petals, ×1.3; E. Labellum and spurs, ×1.3; F. Column, ×4; G. Rostellum, side view, ×4. Drawn by Mary Grierson from *Ball 561*.

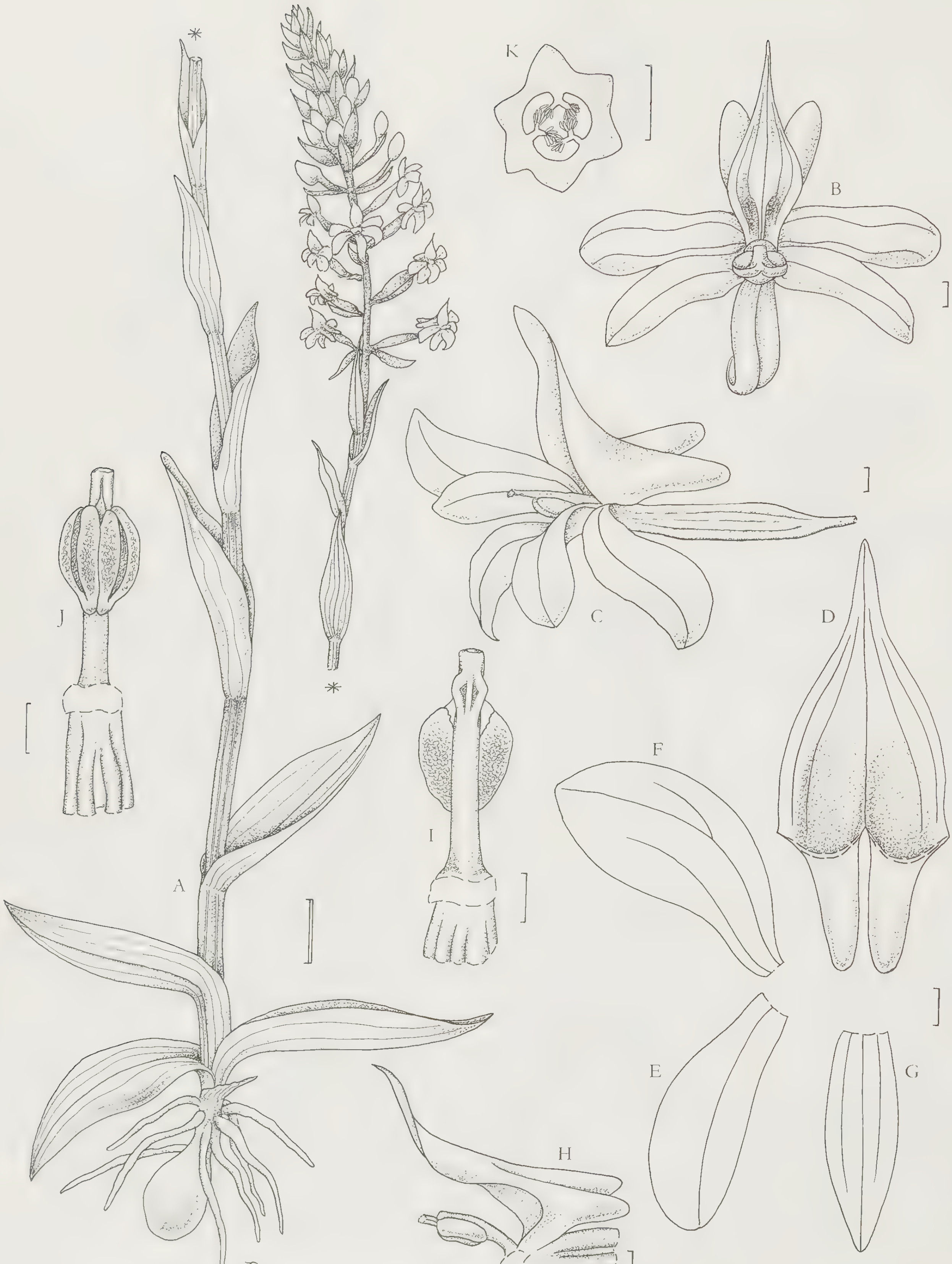

Fig. 18.2. *Satyrium rhynchanthum* Bolus. A. Habit; B. Flower, front view; C. Flower, side view; D. Labellum; E. Petal; F. Lateral sepal; G. Dorsal sepal; H. Labellum and column, side view; I. Column, from above; J. Column, from below; K. Ovary, transection. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Oliver 8612* and Kew Spirit Collection no. 5277.

longer, green, occasionally with white or pink tinge. *Flowers* non-resupinate, comparatively small, in various colours, often with darker markings, often somewhat nodding, with a lower platform made up of the sepals and the petals, which are more or less united basally with each other and the lip or form a short tube with them. *Sepals* and *petals* subequal, free upper parts spreading, reflexed or recurved, lanceolate, lorate, ligulate or ovate, obtuse, entire, rarely petals marginally lacerate, almost always fresh at flowering. *Labellum* normally galeate, galea-entrance small to large, apex frequently extended into a small flap, which is erect, reflexed or inflexed; with two elongate or saccate spurs, spurs rarely massive and cone-like, rarely obsolete, rarely two extra spurs present. *Column* with a short to elongate stalk; anther almost always pendent, obtuse, with two parallel and adjacent thecae, rarely with a prominent apical connective process; pollinia two, sectile, with a short naked caudicle, normally with two viscidia, viscidia occasionally united, rarely only one viscidium present (*S. rhynchanthum*); auricles prominent and sometimes two-lobed; stigma normally on a short to elongate and hemicircular or truncate flap, flat or concave, obtuse or emarginate, rarely apically two-lobed, in *S. rhynchanthum* stigma tripulvinate and situated on a sessile pad; rostellum normally a flat to keeled flap, unlobed, weakly three-lobed or two-lobed with parallel or spreading and short or long arms; weakly three-lobed rostellum frequently with flat appendix; in *S. rhynchanthum* rostellum massive and unlobed. *Capsule* normally glabrous, frequently winged, not twisted, elongate to orbicular; seeds minutely fusiform. (**HK**, **PL**)

Distribution (Fig. 18.3)

The genus comprises 88 species occurring throughout sub-Saharan Africa, found primarily in the temperate and montane areas. The largest concentration of species and the greatest diversity are found in the south-western part of the western Cape Province of South Africa. A few species are also found in Madagascar, Sri Lanka, India, Nepal, Myanmar, and China. (**HK**, **PL**)

Infrageneric treatment

Although the generic delimitation of *Satyrium* has been stable in the past (except for *Aviceps* and *Satyridium*; see below), the infrageneric classification of the genus has been a serious problem for previous taxonomists. The previous infrageneric classification attempts (Lindley 1830–1840; Kränzlin 1897; Schlechter 1901) appear inadequate as the distribution of some of the characters was only incompletely known at the time (for example length and colour of bracts). Other characters emphasized have since been shown to have evolved independently several times (such as leaves basal and adpressed to the ground; Kurzweil and Linder 1999). The infrageneric classification presented below is that of Kurzweil and Linder (1999), which is based on a cladistic analysis of all of the currently available information (morphological, anatomical, palynological), especially characters related to the structure of the rostellum. Nevertheless, a few species had to be excluded from the analysis and were treated as 'imperfectly known species' as no information on them is available. (**HK**, **PL**)

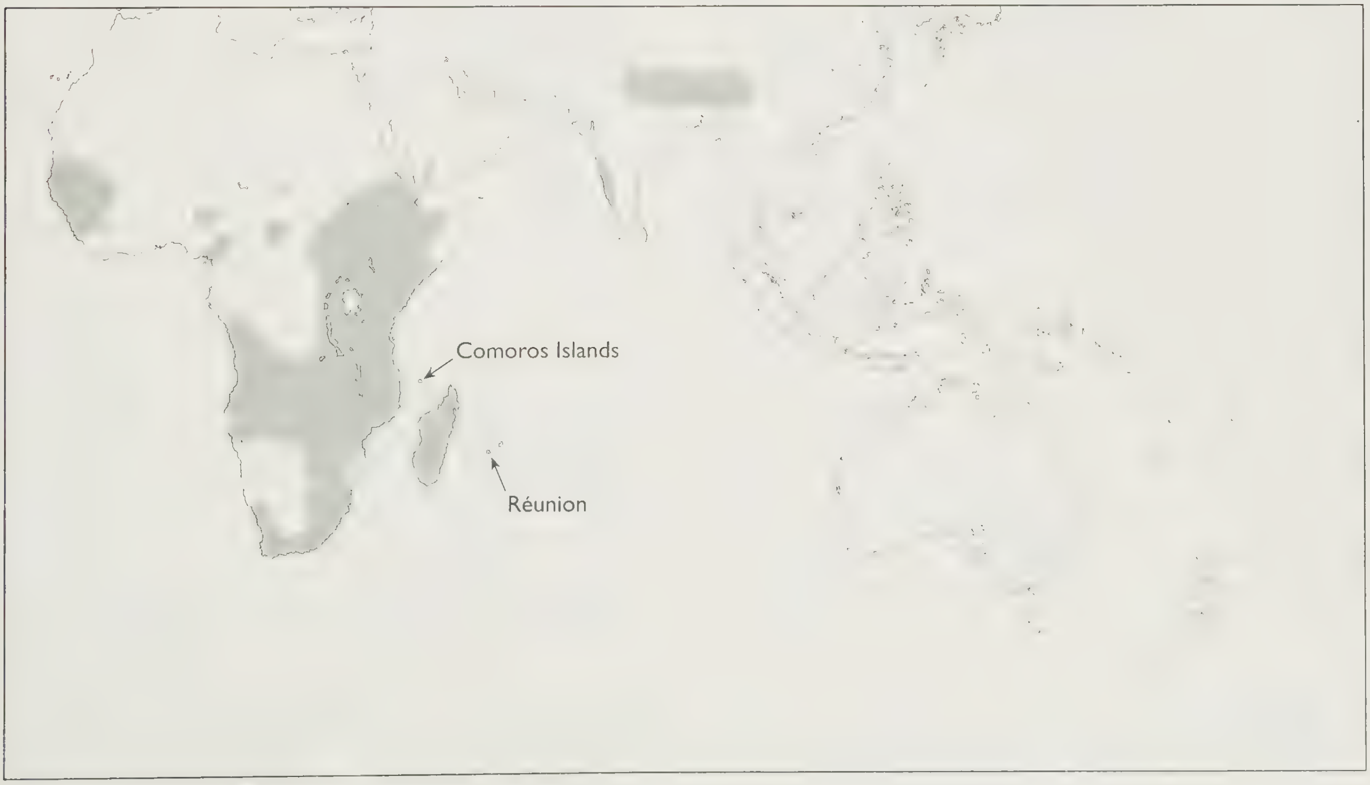

Fig. 18.3. Distribution map of *Satyrium*.

1. **Satyrium** subgenus **Brachysaccium** (Schltr.) Kurzweil & H.P.Linder, *Beitr. Biol. Pfl.*, **71**, 101–81 (1999); Linder and Kurzweil, *Orch. S. Afr.*, 155 (1999). Type species: *S. retusum* Lindl. (lecto.).

Sect. *Brachysaccium* Schltr., *Bot. Jahrb. Syst.*, **31**, 185 (1901).
Sect. *Saccata* Lindl., *Gen. Sp. Orch. Pl.*, 342 (1830–1840), pro parte.
Sect. *Saccatae* Bolus, *J. Linn. Soc., Bot.*, **25**, 195 (1889).

Slender herbs with cauline leaves clustered low on the stem. Inflorescence mostly with spreading bracts, rarely erect or reflexed. Lip galeate with wide entrance, flap usually short or absent, spurs mostly saccate or absent. Anther with short loculi; rostellum three-lobed and mostly with spreading arms, rarely with short and parallel lateral arms; viscidia two, globular. A group of 19 species in sub-Saharan Africa with one species on Madagascar.

2. **Satyrium** subgenus **Bifidum** Kurzweil & H.P.Linder, *Beitr. Biol. Pfl.*, **71**, 101–81 (1999); Linder and Kurzweil, *Orch. S. Afr.*, 163 (1999). Type species: *S. erectum* Sw.

Slender or robust herbs. Leaves cauline or basal, often adpressed to the substrate. Inflorescence lax or dense; bracts mostly reflexed. Lip galeate, entrance wide, flap short or long; spurs slender and filiform, normally longer than the ovary. Rostellum with two parallel and short or long arms. A group of 19 species, widespread in tropical and temperate Africa, with one species in Madagascar.

3. **Satyrium** subgenus **Satyrium** Kurzweil & H.P.Linder, *Beitr. Biol. Pfl.*, **71**, 101–81 (1999); Linder and Kurzweil, *Orch. S. Afr.*, 169 (1999). Type species: *S. bicorne* (L.) Thunb.

Including subsection *Coriophoroidea* Kränzl., *Orch. Gen. Sp.*, 680 (1897), *pro parte*; Sect. *Chlorocorys* Schltr., *Bot. Jahrb. Syst.*, **31**, 174 (1901).

Slender to stout herbs. Leaves basal or cauline, often flat on the ground. Inflorescence few- to densely flowered; bracts mostly reflexed and only rarely erect or spreading, sometimes dry and membranous. Petals normally entire but sometimes with serrate or lacerate margins. Lip galeate, sometimes globose, entrance wide or narrow; apical flap short or long; spurs normally slender-filiform or clavate and longer than the ovary; occasionally two extra short spurs present. Anther normally obtuse, rarely with prominent apical connective process; stigma a flap, in *S. rhynchanthum* Bolus pad-like; rostellum either weakly three-lobed with prominent appendix or entire, almost always with two lateral or subterminal viscidia, viscidium in *S. rhynchanthum* solitary and terminal. Approximately 43 species mainly in tropical and temperate Africa; two species are found in Asia. (**HK**, **PL)**

Cytogenetics

Hall (1982) studied several *Satyrium* species and found that the chromosome number is uniform ($2n = 42$) except in the *S. bracteatum* (L.f.) Thunb. group in which it differs considerably among the species studied. (**HK**, **PL)**

Phylogenetics

In a cladistic analysis (Kurzweil and Linder 1999) of the genus using morphological, anatomical, and palynological characters, the major clades of the tree are mainly based on the rostellum structure, as many other morphological characters are either variable within the species or seem to have evolved several times within the genus. One of the more interesting results is that a species that was previously separated into a monospecific genus *Satyridium* (as *S. rostratum* Lindl.) appears to belong to the clade formally recognized as subgenus *Satyrium*. Although the topology is not well supported, it will be used as the basis of an infrageneric treatment until more information becomes available. It is hoped that molecular data will help in resolving the relationships within *Satyrium*.

Sterile shoots evolved in at least five groups within *Satyrium* (Kurzweil and Linder 1999). Leaves adpressed to the substrate have also evolved in several groups. The same phenomenon is also found in some Orchideae (*Habenaria*, *Holothrix*) and in other plants (*Whiteheadia*, *Massonia*: Hyacinthaceae; *Haemanthus*: Amaryllidaceae). The '*Satyrium*-type' epidermis (Kurzweil *et al.* 1995) is interpreted as a synapomorphy of *Satyrium* and has also evolved in *Holothrix* (Orchideae). The elongate inflorescences as seen in most *Satyrium* species are apparently the basic condition in the genus, and the occurrence of subcapitate inflorescences is consequently derived. As revealed by outgroup comparison the weak-fusion of the sepals and petals is primitive, and the extensive fusion as seen in some species derived. The two lip spurs of *Satyrium* are interpreted as a synapomorphy of the genus (Linder and Kurzweil 1994; the presence of two lip spurs in the Australasian Diurideae genus *Corybas* is a convergence). Saccate lip spurs are probably due to a reduction, which corresponds well with the situation in the subtribe Disinae (Linder and Kurzweil 1990). As a column with a long undifferentiated stalk is the more common state and apparently the basic condition in *Satyrium*, the short stalks of some species are probably derived; however, they seem to have evolved in different groups. The normally pendent anther is almost certainly a synapomorphy of Satyriinae, although it has reversed to an only slightly reflexed anther in one species (*S. bicallosum* Thunb.). Another synapomorphy is the stigma flap, which has reversed to a pad-like stigma in *S. rhynchanthum*.

The structure of the rostellum is an indication of the major lineages within *Satyrium*. Outgroup comparison with Disinae reveals that a three-lobed rostellum is primitive in *Satyrium*, although it is difficult to determine the phylogenetic significance of spreading and parallel lateral arms. Special features such as elongate rostellar arms (e.g. *S. erectum*, *S. pulchrum* S.D.Johnson & H.Kurzweil, *S. foliosum* Sw.) or apical teeth on the lateral rostellar arms (*S. macrophyllum* Lindl., *S. cheirophorum* Rolfe) are almost certainly derived states. Truncate rostellar types are found in four species and are thought to be derived from a three-lobed rostellum with short parallel arms. In the *S. aethiopicum* Summerh. clade, a reduction of the three lobes has taken place, which has reached its final stage in a number of tropical species with an entirely unlobed rostellum. Two separate viscidia are basic in *Satyrium*, although connate viscidia have evolved in several species. The character has reversed in *S. rhynchanthum*, which has an unlobed rostellum with a single viscidium. This character has also evolved independently in *Disa* sect. *Monadenia* (subtribe Disinae).

The analysis by Kurzweil and Linder (1999) identified two clades and a grade, the *S. rhynchantoides* Schltr. clade and the *S. aethiopicum* clade connected by a linking *S. cristatum* Sond. assemblage. Whereas the former two are probably monophyletic, the *S. cristatum* assemblage is most likely paraphyletic.

Subgenus *Brachysaccium* (the *S. rhynchantoides* clade) is largely characterized by a reduction of the spurs. In this group the rostellum has either comparatively short and parallel or spreading arms. The group was already recognized as sect. *Brachysaccium* by Schlechter (1901) and with a similar delimitation as sect. *Saccata* by Lindley (1930–1940) and as sect. *Saccatae* by Bolus (1889). This group, without *S. microrrhynchum* Schltr. and *S. pygmaeum* Sond., was considered an aberrant group from the western Cape of South Africa, which possibly comprises phylogenetically ancient species (Hall 1982). An interesting species is *S. pumilum* Thunb., which was separated into the monospecific genus *Aviceps* as it was thought to lack petals (Lindley 1830–1840). However, clear affinities of *S. pumilum* with *S. bracteatum* were later pointed out, and the species was therefore placed in *Satyrium* (Bolus 1889; Kränzlin 1897; Schlechter 1901; Hall 1982; Kurzweil and Linder 1999).

Subgenus *Bifidum* (the *S. cristatum* assemblage) is largely characterized by parallel rostellum arms and a lip flap that is clearly reflexed. The rostellum arms may be short or long. This group has not been recognized by previous workers, but a few of its species (*S. erectum*, *S. cristatum*, *S. candidum* Lindl., and the *S. macrophyllum* Lindl. complex) were considered closely related (Schlechter 1901; Hall 1982). The position of *S. fimbriatum* is not clear, but the parallel rostellum arms appear to indicate affinities to the group around *S. cristatum*. Alternatively, its dry sheaths and bracts, the lacerate petals and lip flap, and the comparatively long anther canals may also indicate a close relationship to the group including *S. membranaceum* Sw. (*S. aethiopicum* clade).

Subgenus *Satyrium* (the *S. aethopicum* clade) is characterized by a rostellum with reduced three-lobing and two lateral or subterminal viscidia. The entire group has not been recognized previously. However, both Kränzlin (1897) and Schlechter (1901) recognized a group similar to the distinct *S. comptum* Summerh.-*odorum* clade (as *S.* subsect. *Coriophoroidea* and *S.* sect. *Chlorocorys*, respectively). *Satyrium rhynchanthum*, which is here considered 'nested' in the *S. aethiopicum* clade, was previously either split off from *Satyrium* and placed in a monospecific genus *Satyridium* (Lindley 1830–1840; Rolfe 1912–1913; Hall 1982; Linder 1989) or retained in *Satyrium* but placed in a monospecific subgenus or section (Bolus 1889; Kränzlin 1897; Schlechter 1901). **(HK, PL)**

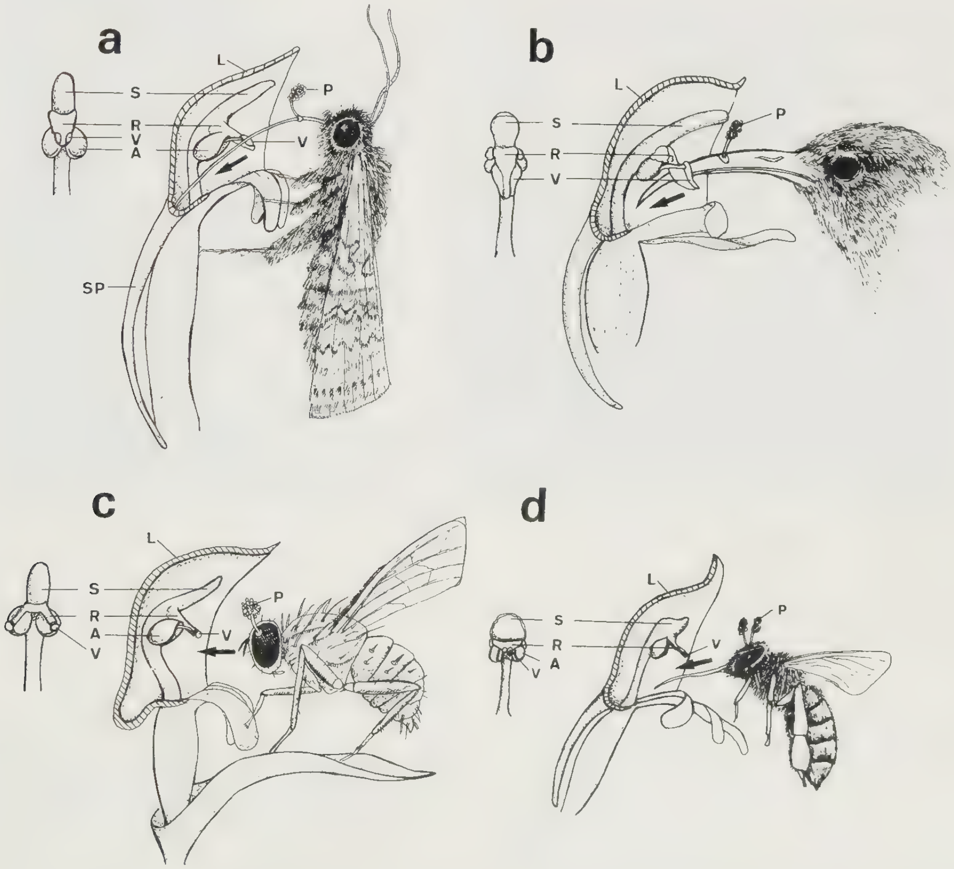

Fig. 18.4. Floral mechanisms in *Satyrium,* illustrated by sections of flowers and a front view of the column. A. Moth-pollinated flower (after *Satyrium bicorne*) with platelike viscidia in lateral rostellum notches. B. Bird-pollinated flower (after *Satyrium carneum*) with large platelike viscidia in lateral rostellum notches. C. Fly-pollinated flower (after *Satyrium bracteatum*) with globose viscidia at the tips of elongated rostellum arms. D. Bee-pollinated flower (after *Satyrium erectum*) with globose viscidia at the tips of elongated rostellum arms (after Johnson 1997*b*).

Ecology

In Africa most species of the genus *Satyrium* grow in full sunlight in open habitats, ranging from fynbos and coastal scrub in South Africa to marshland ('dambos') and montane grasslands in tropical and temperate Africa. A large number of species can also be found in the miombo woodland of central Africa. In South Africa, several species occur in scrubland in the semi-arid Karoo, such as *S. erectum*, *S. pallens* S.D.Johnson & H.Kurzweil, and *S. pulchrum*. In the western Cape of South Africa several species thrive in wet moss on rocks, such as *S. bracteatum*, *S. pygmaeum* Sond., and *S. rupestre* Schltr. Madagascan *Satyrium* species are found in similar habitats as continental African species (Perrier de la Bâthie 1939–1941). In Asia *Satyrium* species are found in high-elevation grassland but occur also in comparatively wet monsoon forest where they have been occasionally reported as epiphytes. In most species flowering is strongly enhanced by veld fires, and a few (the South African *S. stenopetalum* Lindl., *S. bicallosum*, *S. rhynchanthum*) flower only after fire.

Most species of the winter-rainfall area of the western Cape of South Africa flower in spring, whereas the species of the summer-rainfall region (northern and eastern parts of South Africa, tropical Africa, *S. nepalense*) flower in summer. **(HK, PL)**

Pollination

Satyrium shows tremendous floral diversity, and a wide range of pollination systems are represented in the genus, involving carrion flies, fungus gnats, moths, butterflies, bees, and even birds (Garside 1922; Vogel 1954; Johnson 1996*a*, *b*, 1997*b*, *c*).

The morphology of *Satyrium* flowers is unusual in that the labellum is twin-spurred and the flowers are non-resupinate. Consequently the column lies in front of the labellum, between the two entrances to the spurs. To secure nectar from one of the spurs, the pollinator has to move its proboscis, bill or entire body past either side of the column, typically removing one or both pollinaria in the process. Pollinarium placement is nototrobic, typically on the proboscis, bill or head of the pollinator. Johnson (1997*a*) found that the viscidia of those pollinaria adapted for placement on an insect proboscis are flexible and plate-like and seated in lateral rostellum notches (Fig. 18.4A, B), whereas those adapted for placement on the head or eyes of the pollinator are globose and seated at the apex of elongated rostellum arms (Fig. 18.4C, D).

The majority of *Satyrium* species appear to secrete nectar (S. Johnson, unpublished). Pollination by moths seems to be prevalent in the genus, based on the large number of species with night-scented pale flowers with long spurs. Pollination by small settling moths belonging to the family Noctuidae has been documented for several species, including *S. stenopetalum* Lindl., *S. bicorne* (Fig. 18.5E), and *S. longicauda* Lindl. (S. Johnson, unpublished). Pollination by larger hawkmoths is likely to be ubiquitous in long-spurred *Satyrium* species in central Africa. Johnson (1997*a*) found that *S. ligulatum* Lindl. is pollinated by both butterflies and moths, a phenomenon that also occurs in the European orchid *Gymnadenia conopsea* (Darwin 1877).

Satyrium hallackii Bolus exhibits considerable geographical variation in floral traits in southern Africa. Populations in grassland habitats have long spurs (20–36 mm) and are pollinated mainly by hawkmoths, whereas populations in the fynbos of the western Cape have much shorter spurs (8–15 mm) and are pollinated by carpenter bees. Johnson (1997*b*) argued that this floral shift was driven by an ecological gradient in pollinator abundance: hawkmoths are relatively plentiful in grasslands and rare in fynbos, but the reverse pattern is true of carpenter bees, which require woody vegetation such as fynbos to make nests.

Pollination exclusively by bees has been recorded in *S. erectum*, a species with pink fragrant flowers and relatively short spurs (Johnson 1997*a*). The stippled markings (nectar guides) on the petals are similar to those found in many bee-pollinated *Orchis* species. Pollinaria are attached to the head of the bees (Fig. 18.5C, D).

Garside (1922) was the first to show that the diminutive white flowers of *S. bicallosum* are pollinated by small fungus gnats (*Sciara* sp.). He used the novel technique of collecting flies from the sticky leaves of a sympatric *Drosera* species and examining them for pollinaria of the orchid. The flowers of *S. bicallosum* are unusual in having two separate entrances to the labellum.

Satyrium bracteatum and *S. pumilum* conform to the classical syndrome of carrion-fly pollination, known in other orchids such as *Bulbophyllum* and *Masdevallia* (Dressler 1993). They have brown flowers with a fetid odour reminiscent of rotting flesh. Johnson (1997*a*) confirmed that *S. bracteatum* is pollinated by carrion flies, principally *Helina* and *Scatophaga* species and that pollinaria are attached to the eyes of these flies when they contact the elongated rostellum lobes (Fig. 18.5F). No nectar was found in the flowers of *S. bracteatum*, and this species can be considered to be a brood-site mimic, attracting flies that usually lay their eggs in rotting flesh or animal faeces.

Johnson (1996*a*) showed that sunbirds (*Nectarinia* spp.) pollinate three South African *Satyrium* species, namely *S. carneum* R.Br., *S. coriifolium* Sw., and *S. princeps* Bolus. At present, these are the only African orchids known to be bird-pollinated. These species have unusually large, unscented, red or orange flowers with long spurs containing copious quantities of dilute nectar. Inflorescence stems are robust (up to a metre tall in the case of *S. carneum*) and support the weight of perching birds (Fig. 18.5A). The birds probe the flowers with their bills and extract nectar from the narrow spurs with their tongues. The pollinaria have exceptionally large viscidia that adhere firmly to the upper mandible of the bills (Fig. 18.5B). This is necessary as the birds find the presence of pollinaria on their bills irritating and frequently attempt to scrape them off against branches. Hybrids between *S. carneum* and *S. coriifolium* are found at some sites and can be attributed to sunbirds transferring pollen between the two species. Rebelo (1987) observed sunbirds feeding from the flowers of *Satyrium odorum*, but this is clearly a moth-pollinated species with night-scented flowers and tiny pollinaria; thus the sunbird visits to this species can be regarded as opportunistic. **(SJ)**

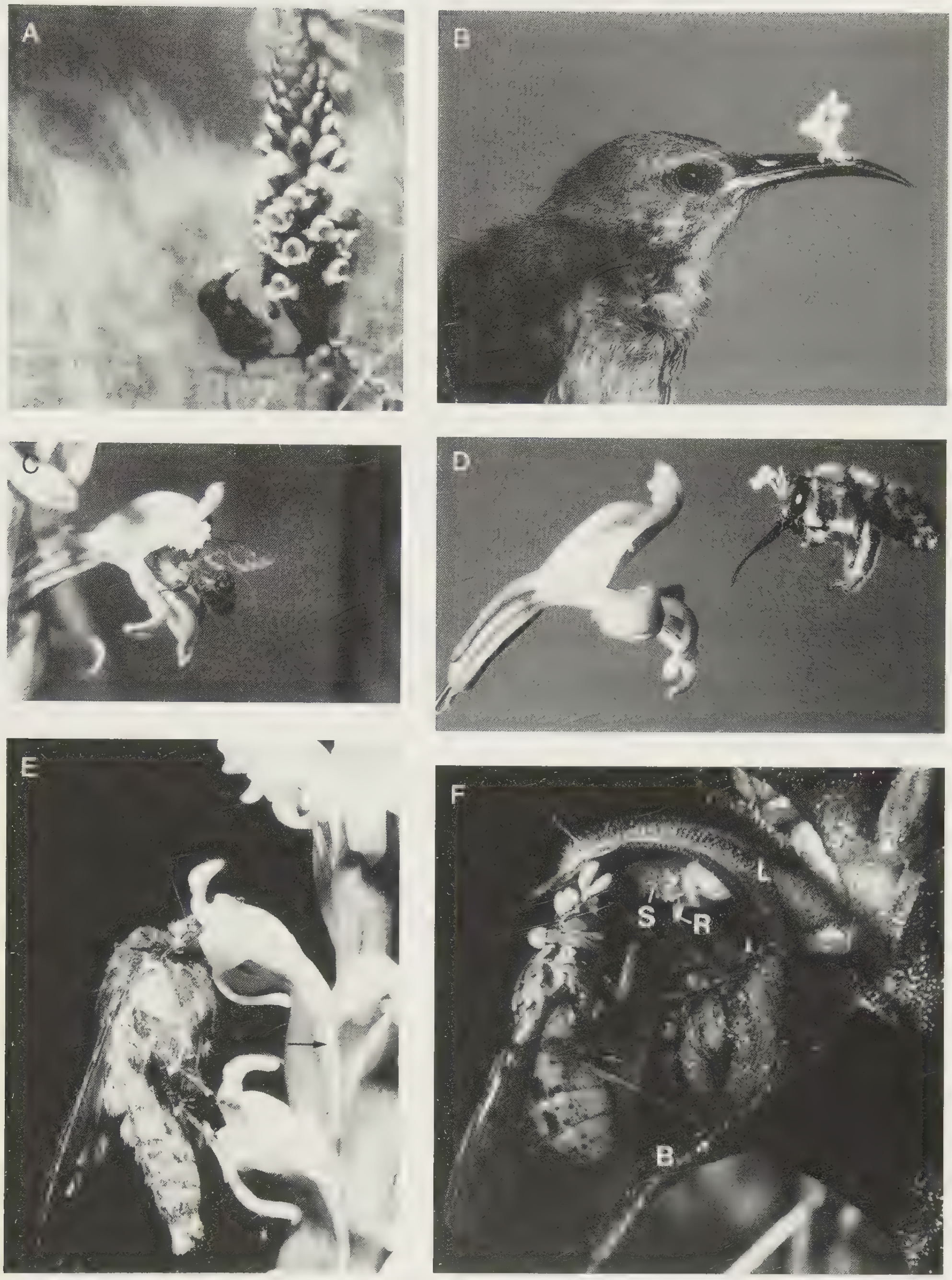

Fig. 18.5. Flowers and pollinators of *Satyrium* species. A. Lesser double-collared sunbird perched on an inflorescence of *Satyrium carneum*. B. Pollinaria of *Satyrium carneum* attached to the bill of a juvenile sunbird. C. Honeybee (*Apis mellifera* subsp. *capensis*) entering a flower of *Satyrium erectum*. D. Anthophorid bee (*Anthophora diversipes*) posed next to a flower of *Satyrium erectum*. Pollinaria are attached to the forehead of the bee. E. Noctuid moth (*Agrotis segetum*) probing the floral spurs of *Satyrium stenopetalum*. F. Carrion fly (*Helina* sp.) entering a flower of *Satyrium bracteatum*. Pollinaria are attached to its eyes.

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B. TRIBE DIURIDEAE

Diurideae (Endl.) Lindl., *Mant. Bot., Suppl.*, **2**, 21 (1842) (as 'Divisio V. Diurideae'); Benth. & Hook.f, *Gen. Pl.*, 463, 483 (1853) (as 'Subtribus Diurideae'); Brieger in Brieger, Maatsch, and Senghas (ed.), *Schlechter, Die Orchideen*, 3rd edn, Band I, Teil A, **1**, 340 (1970); Dressler, *Orch.: Nat. Hist. Class.*, 179 (1981); *Lindleyana*, **1**, 5–20 (1986); *Phylog. Class. Orch. Fam.*, 126–39 (1993); Szlachetko, *Fragm. Flor. Geobot. Suppl.*, **3**, 1–152 (1995). Type: *Diuris* Sm.

Description

Glabrous or hirsute, tuberous or non-tuberous, subterranean or emergent geophytic *herbs*. *Roots* present or absent. *Tubers* globose to elongate, naked or covered wholly or partially by a fibrous tunic. *Leaves* present or absent, one–several, cylindrical or convolute, entire or lobed, petiolate or sessile. *Inflorescence* single-flowered, racemose, spicate or rarely a condensed capitulum. *Flowers* resupinate or non-resupinate, dull to brightly coloured; tepals similar, subsimilar, or dissimilar. *Labellum* fixed, hinged at the base and passively motile or actively motile on the end of an elastic strap, sometimes peltately attached to a rod-like stalk; lamina unlobed or three lobed, unadorned or variously adorned with ridges, rows of sessile or stalked calli, large pseudoglands or trichomes, sometimes in a strongly insectiform arrangement; nectar present or absent. *Column* usually fully united, rarely with stamen and style almost free; column foot present or absent; pollinarium present or absent; pollinia two, four, or eight. *Fruit* usually a dehiscent capsule, rarely an indehiscent berry. **(DJ)**

Distribution (Fig. B.1)

India and Nepal through south-east Asia and Japan to Australia, New Zealand, Fiji, Samoa, and the Society Islands. **(DJ)**

Anatomy

Leaves are spiral, distichous, basal, or absent; convolute to weakly plicate, soft herbaceous to somewhat fleshy and coriaceous, dorsiventral to terete. Adventitious root systems are generally well developed, with some or all of the following, depending on the taxon: absorbing storage roots; droppers (often enclosed in fibrous sheaths, which arise endogenously from undifferentiated cortical parenchyma of the stem base, the previous dropper, the distal pole of the previously formed dropper, or the coalescence of an axillary bud with root primordium on the parent axis; droppers usually grow downward either vertically or obliquely and terminate in replacement root tubers); root-like stolons, originating in the same way as droppers but growing mainly horizontally and terminating in reproductive tubers, leading to the formation of tufts, clumps, or colonies (e.g. *Corybas*); root tubers, or swollen storage roots bearing root buds that produce new shoots and inflorescences; and stem tubers, differentially swollen underground shoots with scale leaves subtending axillary buds (*Rhizanthella*). The following anatomical descriptions and those corresponding to specific subtribes are based on the literature (Pridgeon 1993, 1994*a*, *b*; Pridgeon and Chase 1995) and on otherwise unpublished observations. A list of material examined is available from the author on request.

With some exceptions, characters from vegetative anatomy of underground organs of Diurideae are of limited systematic utility above the genus level (often the species level), so high is the degree of homoplasy (Pridgeon 1994*a*; Pridgeon and Chase 1995). However, some leaf characters such as presence and types of trichomes, cuticular sculpturing, anticlinal walls of epidermal cells, and heterogeneity of chlorenchyma support the segregation of *Lyperanthus nigicans* R.Br. and *L. forrestii* F. Muell. as the genus *Pyrorchis* D. L. Jones & M. A. Clem. (Pridgeon 1994*b*), *Caladenia menziesii* R.Br. as *Leptoceras* (R.Br.) Lindl. (Pridgeon 1993, 1994*b*), and *Caladenia sericea* Lindl. and relatives as the genus *Cyanicula* Hopper & A. P. Brown (Pridgeon 1993, 1994*b*). Such characters, however, do not support the segregation of *Caladenia barbarossa* Rchb.f. and relatives nor the continued separation of *Paracaleana* Blaxell from *Caleana* R.Br. Recent molecular evidence (M. A. Clements, personal communication; Kores *et al.* 2000) confirms this assessment.

Leaf

Leaves dorsiventral to terete. Papillae present, one per cell, in some genera. Hairs, if present, of three main types: multicellular glandular, multicellular nonglandular, and bi- to triseriate glandular (*Aporostylis*; Caladeniinae). All hairs are unbranched. Cuticle variously sculptured, most often striate. Epidermis with rectangular to polygonal cells, anticlinal walls sinuous or straight, thin- or thick-walled, with or without conspicuous pit-fields. Stomata superficial, on one or both surfaces; outer and inner ledges very small, more or less equally developed. Hypodermis present only in *Praecoxanthus* (Caladeniinae). Mesophyll homogeneous or heterogeneous depend-

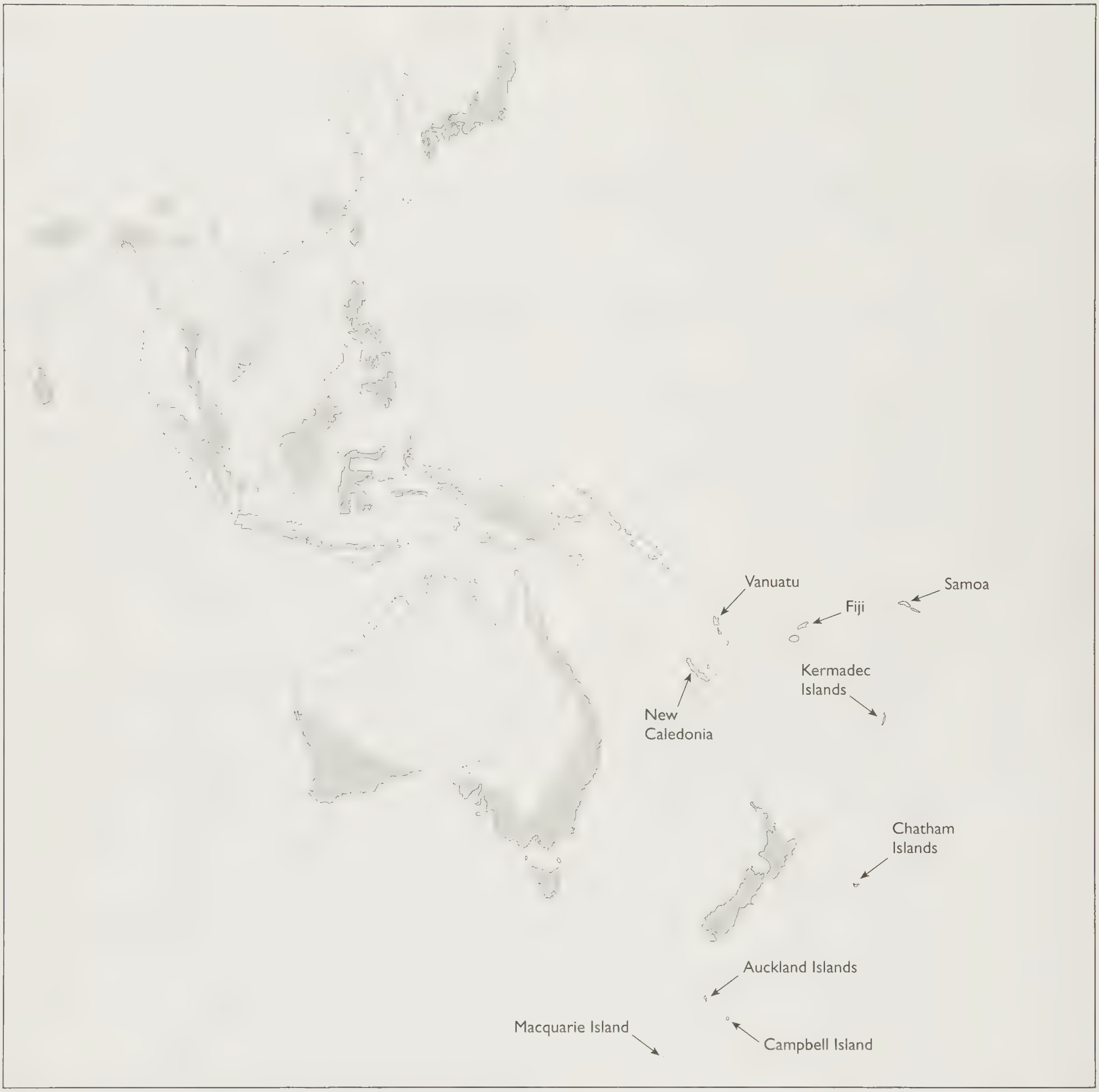

Fig. B.1. Distribution map of Diurideae (partial range; see text).

ing on taxon. Vascular bundles collateral, generally in one row in centre of mesophyll. Sclerenchyma bundle caps mostly absent, and bundle-sheath cells mostly thin-walled. Stegmata absent. Crystals either rod-shaped or raphides, in assimilatory cells or mesophyll idioblasts.

Stem

Stem often differentiated into two regions: 1) an aerial portion sometimes with multicellular hairs and a ring or sheath of mechanical tissue in the inner cortex, and 2) a basal, barely subterranean portion 'collar') with multicellular, mycorrhizal hairs (Fig. B.2), cortical infection zones, and an endodermis with casparian strips. Cuticle usually thin, striate. Stomata present or absent depending on the taxon. Vascular bundles collateral, usually in 1 or 2 rings. Stegmata absent.

Tuber

Root tubers more or less cylindrical to globose, often enclosed in a few to multilayered fibrous sheath, extending up the dropper as well in some species. Hairs present or not, if present usually multicellular and associated with mycorrhiza. Velamen or simple epidermis depending on taxon. Exodermis one-layered. Tilosomes absent. Ground tissue parenchymatous, filled with starch grains in new tubers.

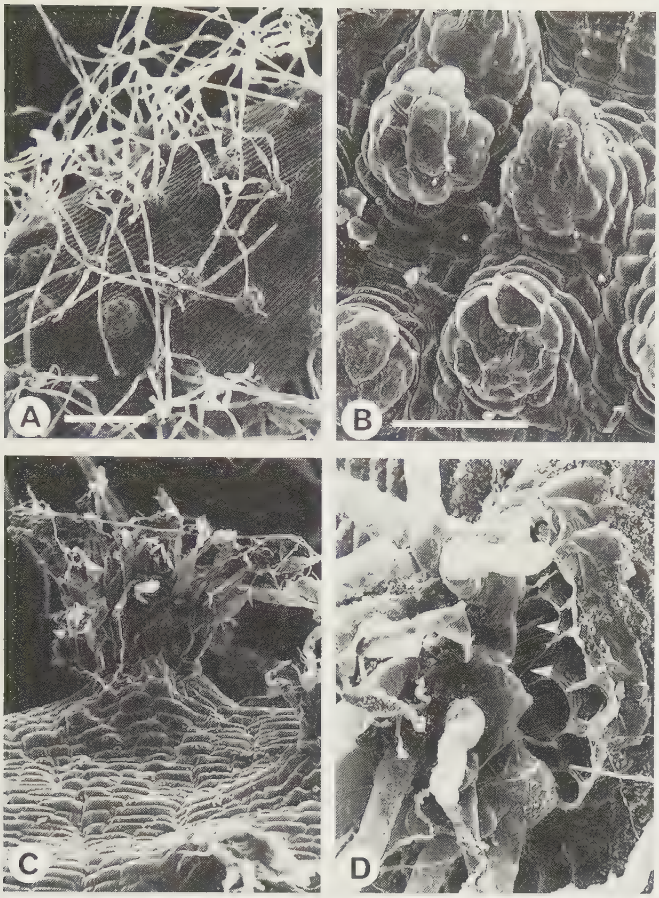

Fig. B.2. Scanning electron micrographs. A–B *Caladenia latifolia*. Collar of emerging shoot showing trichomes at different stages of development, some still dividing, while others have completed development and have elongate apical cells. A: scale bar = 250 μm. B: scale bar = 100 μm. C–D *Pterostylis nutans*. Mature collar with apical cells of trichomes associated with fungal hyphae. C: scale as in A. D: note intrusion of hyphae (arrows) beneath dehiscing apical cells. Scale as in B. Reproduced by permission of the Trustees of The Royal Botanic Gardens, Kew, from *Kew Bulletin*, 49 (3), 569–79.

Endodermis one-layered with casparian strips. Pericycle as for root. Stele dissected or not depending on taxon. Xylem and phloem cell types as above. Crystals in ground tissue either rod-shaped or raphides.

Stem tubers (*Rhizanthella* only) with a thick, heavily suberized cuticle, lacking hairs. Epidermal cells elliptical to polygonal, outer wall slightly thickened. Stomata absent. Ground tissue parenchymatous, cells with relatively thick walls and large nuclei, some cells infected with pelotons. Vascular bundles collateral, in one ring. Xylem tracheids with helical or scalariform thickenings. Ergastic substances not observed.

Root

Root hairs unicellular, multicellular-uniseriate, or multicellular-multiseriate, usually associated with mycorrhiza; unbranched. Velamen 1–3-layered in most taxa. Simple epidermis in Acianthinae, some Prasophyllinae, and *Glossodia* (Caladeniinae). Tilosomes absent. Exodermis one-layered. Cortex parenchymatous. Endodermis one-layered with casparian strips. Pericycle one-layered, cells elliptical to polygonal and thin-walled. Stele medullated. Xylem tracheids with various thickening patterns. Phloem with sieve-tube elements, companion cells, and parenchyma.

Root-like stolon

Often furnished with mycorrhizal hairs. Velamen or simple epidermis depending on taxon. Exodermis one-layered. Tilosomes absent. Cortex: cells often with secondary, banded, suberized wall thickenings, especially in Caladeniinae. Endodermis one-layered with casparian strips. Pericycle as for root. Stele dissected or not depending on species. **(AP)**

Palynology

Reichenbach (1852) was perhaps the first to publish observations on the pollen of *Diuris*, *Epiblema*, *Spiculaea*, *Lyperanthus*, *Glossodia*, *Acianthus*, *Microtis*, *Thelymitra*, *Chiloglottis*, *Eriochilus*, and *Prasophyllum* among other genera. The most recent study of pollen of Diurideae is that by Ackerman and Williams (1981). According to their reports, pollen unit and morphology within and among Acianthinae, Diuridinae, Prasophyllinae, and Caladeniinae *s.l.* are diverse. Sculpturing is also diverse, from foveolate to reticulate. Within Caladeniinae *s.l.*, the exine of *Drakaea* and *Spiculaea* is scabrate, whereas that of other genera is finely reticulate. This difference and strong evidence from ITS sequences of rDNA (M. Clements, personal communication) support Dressler's (1993) reinstatement of Drakaeinae Schlechter, encompassing these genera as well as *Arthrochilus*, *Caleana*, and *Chiloglottis*. Specific reports of pollen morphology, if available, are provided below under generic headings. Much more work is clearly needed here to supplement anatomical and molecular evidence. **(AP)**

Cytogenetics

Few chromosome counts have been reported for members of Diurideae, a significant gap in our knowledge of the group. In his general review of cytogenetics of Orchidaceae, Brandham (1999) could find only three published counts for the group: *Corybas* ($2n = 40$), *Cryptostylis* ($2n = 42$), and *Microtis* ($2n = 44, 88$). **(AP)**

Phylogenetics

Historically the recognition and circumscription of the tribe Diurideae is replete with change. Lindley (1840) created 'Diuridae' (as a Division), placing it in the tribe Neottieae (= subfamily Neottioideae) based on the possession of a single dorsal anther, with powdery, granular, or sectile pollen. He included *Diuris*, *Orthoceras*, *Prasophyllum*, *Burnettia*, and *Genoplesium* within his concept of Diurideae. Concurrently he recognized a second Division, Thelymitrideae ('Thelymitridae'), in which he included *Thelymitra* and *Epiblema*, separating these taxa on differences in column morphology. Endlicher (1842) copied almost *verbatim* Lindley's classification of the family Orchidaceae, while treating the tribes as suborders (= subfamilies) and sections and divisions as tribes

(Butzin 1971). Thus, almost by default, Endlicher established the tribe Diurideae based on Lindley's concept of this taxon.

Thereafter Bentham and Hooker (1883) treated the Diurideae as one of six subtribes within the tribe Neottieae (= subfamily Neottioideae) based on the possession of a single, erect, operculate, persistent anther with distinct parallel loculi; granular, sectile pollinia; and bulbless stems. Under this expanded circumscription they included 24 genera in three informal groups: 1) Asiatic, leafless herbs with short rostellum, viz. *Lecanorchis*, *Aphyllorchis*, *Stereosandra*; 2) Australasian genera with one to a few leaves (rarely leafless), glandular pollinia, pendulous rostellum adhering to a stipe, viz. *Thelymitra*, *Epiblema*, *Diuris*, *Orthoceras*, *Cryptostylis*, *Prasophyllum*; and 3) Australasian genera similar to group 2 but with a short column, pollinia affixed dorsally to rostellum, viz. *Microtis*, *Corysanthes*, *Pterostylis*, *Caleana*, *Drakaea*, *Acianthus*, *Eriochilus*, *Lyperanthus*, *Burnettia*, *Cyrtostylis*, *Caladenia*, *Glossodia*, *Adenochilus*, *Chiloglottis*, and *Calochilus*.

The German morphologist Pfitzer (1882, 1889) proposed a new system of classification of the family that recognized the significance of anther number as a key factor in determining phylogeny. As a result he treated those taxa possessing three or two anthers first and interpreted these characters as indicative of the more 'primitive' nature of these taxa than those with a single anther. Within Pfitzer's system he grouped all terrestrial taxa with an acrotonic anther, including Diurideae, as one of 14 subtribes within tribe Neottieae (as Neottiinae). Here for the first time we see Chloraeinae linked to the Diurideae.

Schlechter used Pfitzer's classification system as a basis for his own system wherein he placed greater emphasis on the structure of the pollinia as a means for determining relationships. Schlechter (1926) deviated little from Pfitzer's work, treating the same group of taxa, including Diurideae (as a subtribe), within tribe Polychondreae, which was equivalent to Pftizer's tribe Neottiinae.

Mansfeld (1937) disputed Schlechter's interpretation of the significance between mealy and waxy pollinia as a means of separating major groups of orchids. On this basis, Mansfeld modified tribe Neottieae (= Polychondreae) by excluding individual genera from subtribes Tropidiinae (placing them in Sobraliinae of Epidendreae) and Pogoniinae (placing them in Vanillinae). He treated Acianteae, Megastylideae, and *Chiloglottis* within Caladeniinae, Prasophylleae within Thelymitrinae, and Drakaeinae (except for *Chiloglottis*) within Pterostylidinae. Mansfeld's concept of tribe Neottieae therefore contained 18 subtribes, including Caladeniinae, Diuridinae, Thelymitrinae, Cryptostylidinae, Corybasinae, and Pterostylidinae (Mansfeld 1954).

Dressler and Dodson (1960) published a review of the classification of Orchidaceae, while simultaneously updating the nomenclature of many higher level taxa to conform to the *International Code of Botanical Nomenclature* resulting from changes passed at the 1959 International Botanical Congress. In updating the classification, including delimitation of tribes, they relied heavily on the interpretations of pollen, pollinium, and pollinarium morphology. In their system of classification, tribe Neottieae (subfamily Orchidoideae) contained nine subtribes, viz. Chloraeinae, Rhizanthellinae, Pterostylidinae, Neottiinae, Diuridinae, Cryptostylidinae, Prasophyllinae, and Spiranthinae. It was characterized as those taxa with 'anther more or less erect, often dorsal (terminal and operculate in some species of *Acianthus*); stems without corms or other thickenings'. The inclusion of Rhizanthellinae was new as was the reduction of subtribes Caladeniinae, Thelymitrinae, Acianthinae, Corysanthinae, and Megastylidinae to synonymy with Chloraeinae on the basis of presumed overall similarity of *Caladenia* with the South American *Codonorchis* and *Chloraea*.

It was Brieger (1971) and Dressler (1972) to whom we owe the broader and possibly only legitimate concept of tribe Diurideae. In his assessment of the family Brieger informally defined tribe Diurideae, including within it six subtribes: Rhizanthellinae, Diuridinae, Corybadinae, Codonorchidinae, Caladeniinae, and Drakaeinae.

Shortly thereafter Dressler (1974), with heavy reference to results of a numerical analysis on the Australian members of the Neottieae by Lavarack (1971), also attempted to define Diurideae. Dressler grouped together all former members of tribe Neottieae, that is those possessing 'root-stem tubers' and non-massulate pollinia, into tribe Diurideae. His concept of Diurideae included subtribes Acianthinae, Caladeniinae, Chloraeinae, Diuridinae, Prasophyllinae, and Pterostylidinae. He placed Rhizanthellinae in tribe Gastrodieae among the epidendroid tribes. Through a series of papers dealing with the classification of the family, Dressler has continued to maintain this general concept of Diurideae with one notable exception. In his most recent classification he included the Rhizanthellinae within Diurideae while also re-recognizing subtribes Drakaeinae and Thelymitrinae as distinct from Caladeniinae and Diurideae on the basis of unique column morphologies.

Alternative systems of classification have been proposed by various authors based on either phylogenetic analysis of morphological features, notably Burns-Balogh and Funk (1998*a*, *b*) and Szlachetko (1995). In these papers, the composition and position of Diurideae has been altered, sometimes radically, from that presented by Dressler (1972, 1981, 1986, 1993). As a result of their phylogenetic analysis of the family, Burns-Balogh and Funk (1986*a*) proposed that elements of Diurideae reside in three separate subfamilies. In their system Diurideae, Prasophylleae, and Cranchideae (which included Cryptostylidinae) formed subfamily Spiranthoideae; Geoblasteae (Caladeniinae, Chloraeinae), Pterostylideae, Thelymitreae, and Neottieae (including Rhizanthellinae) constituted subfamily Neottioideae; and Acianthinae was assigned to the Triphoreae within subfamily Epidendroideae. By comparison, in Szlachetko's radical system of classification, which is based primarily on study of column morphology, all of the elements of Diurideae are found dispersed in the tribes and subtribes of his subfamily Thelymitroideae, which he had separated earlier (1991) from subfamily Orchidoideae. Independent studies on reproductive biology (Clements 1995) and molecular analysis of the plastid gene *rbcL* (Kores *et al.* 1997) and the ITS sequences of nuclear ribosomal DNA (Clements *et al.*, in preparation) almost entirely refute the phylogenetic hypotheses of Orchidaceae as proposed by Szlachetko (1991, 1995). Indeed they show, among other things, that Thelymitroideae, being an independent clade distinct from Orchidoideae is in fact unequivocally sister to Orchideae within Orchidoideae. Moreover, Szlachetko's concept of Thelymitroideae (1991), in which he singled out five tribes (Diurideae, Microtideae, Thelymitreae, Geoblasteae, and Pterostylideae) and his revised concept (Szlachetko 1995), are both polyphyletic.

The monophyly of Diurideae has recently been evaluated through independent studies on embryogenesis (Clements 1995, 1996) and molecular analysis using the plastid genes *rbcL* (Kores *et al.* 1997) *and matK* (Kores *et al.* 2000) and ITS sequences (Clements *et al.*, in preparation). These studies have shown that Diurideae are polyphyletic as long as Chloraeinae (including Geoblasteae) and Pterostylidinae are maintained therein and that these subtribes are more closely related to Cranichideae. Clements (1995) and Molvray *et al.* (2000) established that *Rhizanthella* was unequivocally part of Diurideae, that *Geoblasta* (on which the Geoblasteae is based) is merely part of Chloraeinae, and that Chloraeinae (excluding *Megastylis*) is also better placed near Cranichideae. These same studies have also shown that Diurideae should be treated as comprising subtribes Acianthinae, Caladeniinae, Cryptostylidinae, Diuridinae, Drakaeinae, Megastylidinae, Rhizanthellinae, Prasophyllinae, and Thelymitrinae. **(MAC)**

Cultivation

The majority of Diurideae occur in the temperate areas of Australia that have a 'Mediterranean' type climate, i.e. cool, damp winters and hot, dry summers. They have an annual growth cycle governed by the seasons. During the hot, dry summers, most Diurideae are dormant, surviving underground in the form of a tuber. At the onset of autumn rains the tuber produces one or more leaves and a few roots. The plant's growth continues through winter and spring, when flowers are produced, pollination effected, and seed dispersed. By the end of spring the above-ground parts of the plant dry off. Underground portions of the stem or roots have been colonized by mycorrhizal fungi, which help in supplying some nutrients. Some Diurideae are more heavily dependent upon this mycorrhizal relationship than others, and this is generally reflected in their success in cultivation. During their growth period, a replacement tuber and/or daughter tubers are produced, and at the end of the growing season the old tuber withers away, leaving the new ones to lie dormant over summer. Species that make a replacement tuber only are termed solitary species, whereas those that produce replacement and/or daughter tubers are colony-forming species.

Potting mix

The mix needs to be well drained but retain sufficient moisture for plant growth. Excessive moisture retention can lead to tuber rot. Many successful mixes contain various components such as sphagnum moss, leaf mould, peat moss, perlite, various grades of sand, commercial potting mix, polystyrene beads, and loam.

A basic starting mix used successfully by growers in Australia for many years comprises leaf mould (1 part), wood shavings (not western red cedar or treated pine; 1 part), friable loam (1 part), and coarse sand (particle size approx. 2–4 mm; 2 parts) with a small portion of slow-release nitrogenous fertilizer such as blood and bone. Leaf mould provides immediate nutrients for the plants and mycorrhizal fungi. Wood shavings are a longer-term source of nutrients as they are broken down more slowly, and their structure promotes drainage. Loam aids in moisture retention and provides essential plant nutrients. The coarse sand facilitates drainage. As microorganisms proliferate in this mix, the nitrogenous fertilizer prevents nitrogen deficiency. The proportions of this mix can be varied according to the grower's particular climate, growing conditions, and species being grown.

Most Australian soils contain low levels of phosphorus. Mycorrhizal fungi are sensitive to high levels of phosphorus, so commercial potting mixes should be used with caution as the higher concentrations of fertilizers can be detrimental to the growth of both plant and mycorrhizal fungi. If available, potting mixes without added fertilizer can be tried. These appear suitable for the easy-to-grow, colony-forming species, provided some extra coarse sand is added to improve drainage. Perlite has also been used successfully as an inert drainage material.

pH

Most Australian soils are acidic, many in the pH range of 4.0–5.0. Some soils, however, are of calcareous origin and are neutral or basic, so an adjustment of the pH of the mix is important. This can be achieved by using lime, limestone, or dolomite. Mixes can be made more acidic by the addition of a small amount of sulphur. Simple pH testing kits should be readily available from a local plant nursery.

Containers

The size of a container affects the moisture retention in the mix. When in growth terrestrial orchids require the moisture level to remain more or less constant, so containers of less than 10 cm in diameter are not recommended as they dry out too quickly. A 15-cm pot is an ideal size. Allowances also have to be made for the material from which the pot is made. Plastic pots are non-porous and light to carry around, whereas terracotta pots are porous, faster to dry out, and heavy.

Light

Light requirements vary according to the species being grown. The extremes are represented by *Corybas* (growing in shade) and *Thelymitra* (full sun). Many diurids grow in about 50% shade. When light is excessive the plants respond with stunted growth and yellowing of leaves. Dark green 'leggy' plants and poor flowering indicate insufficient light.

Growing area

Plants are best grown in an area where watering can be controlled but which is well ventilated, for example a greenhouse with a solid translucent roof and shade-cloth walls. One or more walls made of a solid translucent material may be necessary to provide further protection. Shade-cloth can be added to or removed from the roof according to the season. A shadehouse also affords some protection from frosts. In colder climates, some terrestrials have been successfully grown indoors under lights. If plants are grown in an area not protected from rainfall, extra care should be taken to ensure that the pots drain well as waterlogging will result in tuber rot.

Temperature

Most Diurideae in cultivation are tolerant of a wide range of temperatures but need to be protected from heavy frosts.

Watering

Plants are kept evenly damp during their growing period, which for most species is from autumn through winter and spring. When the plant goes into its dormant phase, watering should cease because excess moisture during this time is likely to lead to rotting of the dormant tubers. Usually it is just necessary to sprinkle pots occasionally to prevent tuber desiccation. Some species grow and flower through summer and have a short or no dormant period, so watering of these must continue while they are in active growth—they are kept damp for almost 12 months of the year. When commencing watering after the dormant period, the potting mix is dry and inclined to repel moisture; check that the mix has become totally damp and that the centre of the pot is not still dry. Dried organic material and some fine sands and soils are notoriously hard to rewet. Extra coarse sand in the mix helps to alleviate this problem.

Potting and repotting

The number of tubers in a pot depends on the size of the tuber, e.g. 15–30 tubers of *Acianthus* or *Chiloglottis* would grow well in a 15-cm pot, whereas 10 large *Diuris* tubers would probably be too crowded. Overcrowding in pots leads to smaller replacement tubers and poor growth.

Colony-forming species quickly fill a container and are best repotted yearly or at most every two years for optimum plant growth. Solitary species may be left to grow undisturbed for several years. Most potting mixes such as the basic mix contain organic materials that are gradually broken down by microorganisms, resulting in a smaller particle size and hence poor drainage. It is therefore good practice to replace half of the old mix with new mix every 1–3 years. Some species benefit from not being disturbed too frequently, e.g. many *Caladenia* species, and are left for at least three years. Their mix generally contains more inert draining material, so the particle size is more stable.

Propagation

Colony-forming species propagate themselves, so the annual repot is the time to harvest excess tubers and distribute or grow on. Solitary species in the wild are propagated by germination of seed only. Many solitary species in cultivation, however, can be induced to grow a second and sometimes more replacement tubers. The plant is gently removed from its container at about 5–6 months into its growing cycle, which for many species is at flowering time. The new tuber is carefully twisted or cut off, taking care not to break the old tuber off the stem, and the old tuber and plant repotted. Another new tuber or more will grow from dormant buds at the base of the stem, provided plant growth can be maintained for another 2–3 months. The first new tuber removed is mature enough at this stage to grow the following season. This procedure has not been successful with *Caladenia*.

Seed can be germinated around parent plants. In theory, the mycorrhizal fungi necessary for germination of seed is present with the adult plant. Seed is best sown in autumn when the mycorrhizal fungi become active. Seedlings generally appear about five months later. A mulch on the top of the pot provides a humid environment to protect the newly emerging fine seedlings. The top of the pot needs to remain damp enough to prevent dehydration of the seedings but not so wet that damping off occurs. It is best not to disturb the pot for at least another growing season so that the tiny first-year tubers are given time to increase in size during the second season.

Research into the laboratory propagation of Diurideae and other Australian terrestrial orchids has been carried out intensively in recent years at Kings Park and Botanic Garden in Western Australia. The researchers there have a preference for symbiotic germination and have virtually perfected the technique for deflasking seedlings. They are working on the translocation of their propagated seedlings for conservation purposes. Commercially, there are only a few people who flask terrestrials, and there has not been a wide range available. Consequently, growers have had limited experience in deflasking. A sphagnum moss and polystrene bead mix has worked quite well for the initial deflasking, but young plants seem to do better in a soil-based mix after about 12 months.

Pests

The usual orchid pests—aphids, scale, two-spotted mites, thrips, snails, slugs, caterpillars—can attack plants at any stage of development. Damping-off and leaf rots can also occur, generally indicating excessive moisture or lack of ventilation. Rusts will also sometimes infect plants, as will viruses. **(HR)**

SUBTRIBE ACIANTHINAE

Acianthinae (Lindl.) Schltr., *Bot. Jahrb. Syst.*, **45**, 381 (1911). Type: *Acianthus* R.Br.

Tribe Acianthidae Lindl., *Veg. Kingd.*, 182 (1846), *nom. nud.*

Subtribe Corybasinae Schltr., *Repert. Spec. Nov. Regni Veg.* **19**, 19 (1923) (Corybaseae). Type: *Corybas* Salisb.

Subtribe Corysanthinae Schltr., *Notizbl. Bot. Gard. Berlin-Dahlem*, **9**, 570 (1926) (as Corysantheae). Type: *Corysanthes* R.Br.

Artificial key to the subtribes of Diurideae (DJ)

1. • Plants wholly subterranean; flowers spirally arranged in a condensed capitulum surrounded by fleshy floral bracts; fruit indehiscent; seeds sclerotic, not winged . . . . . **Rhizanthellinae**
• Plants with subterranean root systems and emergent scapes and/or leaves; flowers solitary or in a spike or raceme; floral bracts thin-textured to membranous; seeds non sclerotic, with a clathrate wing 2

2. • Underground system consisting of fleshy roots without tubers; leaves lasting more than one season 3
• Underground system consisting of fleshy tubers with or without filamentous roots; leaves lasting one season only 4

3. • Flowers non-resupinate; labellum fixed and immobile . . . . . **Cryptostylidinae**
• Flowers resupinate; labellum hinged at the base and passively motile . . . . . **Megastylidinae**

4. • Plants bearing trichomes on most parts; trichomes with a swollen basal cell . . . . . **Caladeniinae**
• Plants glabrous or with trichomes on the floral parts; trichomes, if present, lacking a swollen basal cell 5

5. • Column with stamen and style almost completely free . . . . . **Diuridinae**
• Column with stamen and style completely fused 6

6. • Leaves absent or reduced to bracts or scale leaves 7
• Leaves present 8

7. • Bracts enlarged, leaf-like, reddish to purplish; flowers resupinate . . . . . **Megastylidinae**
• Bracts reduced and scale-like, colourless; flowers non-resupinate . . . . . **Drakaeinae**

8. • Leaves two–six per shoot, either basal around the scape or in a lateral rosette . . . . . **Drakaeinae**
• Leaf one per shoot, always basal 9

9. • Leaf cylindrical 10
• Leaf convolute 11

10. • Labellum similar or subsimilar to the other perianth parts; pollinia white, attached directly to a viscidium . . . . . **Thelymitrinae**
• Labellum markedly dissimilar to the other perianth parts; pollinia yellow, attached to the viscidium via a hamulus . . . . . **Prasophyllinae**

11. • Labellum fixed and immobile 12
• Labellum actively or passively motile 14

12. • Plants single-flowered; flower dominated by the dorsal sepal and labellum; column enclosed in labellum tube . . . . . **Acianthinae**
• Plants usually multi-flowered; flower not dominated by the dorsal sepal and labellum; column exserted 13

13. • Leaf much longer than wide, broadly to deeply channelled; pollen white . . . . . **Thelymitrinae**
• Leaf as wide as long or not much longer than wide, flat; pollen yellow . . . . . **Acianthinae**

14. • Labellum actively motile, attached by a thickened sensitive strap . . . . . **Drakaeinae**
• Labellum passively motile, hinged with a short membranous strap 15

15. • Column foot absent or rarely vestigial; labellum not insectiform . . . . . **Megastylidinae**
• Column foot well developed; labellum strongly insectiform . . . . . **Drakaeinae**

Description

Glabrous, tuberous geophytic *herbs*. *Tubers* small, globose, naked. *Leaf* solitary, convolute, sessile or petiolate, as wide as long or nearly so, erect to prostrate, entire or lobed, thin to membranous. *Inflorescence* single-flowered or racemose. *Flowers* resupinate, dull-coloured, either solitary on a short peduncle and dominated by the dorsal sepal and labellum with the column enclosed in the labellum tube or 1–several on a relatively long scape with all tepals subsimilar and the column exserted. *Labellum* unlobed, fixed to the base of the column, either with a tubular base and spreading lamina or flat and plate-like, with or without basal calli; nectar present or absent. *Column* lacking free filament and style; column foot absent; pollinarium present or absent; pollinia four. *Fruit* a dehiscent capsule. **(DJ)**

Anatomy

Leaf

SURFACE

Hairs absent. Epidermis: cells polygonal; walls thin (except moderately thick with conspicuous pit-fields in *Townsonia*), sinuous in *Acianthus* and often sinuous in *Corybas*. Stomata on abaxial surface only, guard-cell pairs remarkably large in *Cyrtostylis* (92 μm long, 98 μm wide) and *Corybas macranthus* (Hook.f.) Rchb.f. (88 μm long, 88 μm wide).

TRANSECTION

Cuticle thin, smooth to striate at margins in *Acianthus*, minutely punctate with radiating ridges in *Cyrtostylis*, micropapillate to ridged adaxially in *Corybas*, minutely punctate in *Townsonia*. Epidermis: cells isodiametric, elliptical to polygonal; outer wall thickened. Adaxial cells usually larger than abaxial cells; in *Cyrtostylis* adaxial cells large, occupying about half of the leaf volume, the abaxial cells about one quarter. Stomata superficial (slightly elevated in *Cyrtostylis*), substomatal chambers shallow. Mesophyll homogeneous in all taxa except *Cyrtostylis* with two palisade layers. Vascular bundles as for the tribe. Crystals: raphides in mesophyll idioblasts, druses in epidermis of *Cyrtostylis*.

Collar/stem

TRANSECTION

Hairs on collar multiseriate, associated with mycorrhiza, in *Acianthus*, some species of *Corybas*, and *Townsonia*; uniseriate, buttress-type hairs in *Cyrtostylis* and some species of *Corybas*. Cuticle thin, smooth. Epidermis: cells elliptical to polygonal, anticlinally elliptical in *Townsonia*; outer wall thickened. Stomata present only in *A. sublestus* Dockrill. Ground tissue parenchymatous, outer layers often infected with hyphae and pelotons. Outer 3–5 layers in *Townsonia* disrupted with large lacunae; inner 1–2 layers sclerotic, forming a sclerenchyma sheath. Endodermis of collar: cells elliptical to polygonal. Vascular bundles collateral, in one ring (with smaller bundles in flanges in *Corybas*). Stele of collar medullated, 4–13 arch. Xylem tracheids mostly with helical or scalariform thickenings. Crystals: raphides in ground tissue.

Tuber

TRANSECTION

Hairs unicellular on single-layered sheath enclosing tuber; hairs absent in *Corybas* except uniseriate, buttressed type in *C. unguiculatus* (R.Br.) Rchb.f. Velamen 1–2 layered, cells elliptical to polygonal, periclinally compressed. Walls suberized, of uniform thickness, but outer and/or radial walls thicker in *Acianthus*. Exodermis: cells isodiametric to polygonal; walls suberized, of uniform thickness or differentially thickened depending on taxon. Ground tissue parenchymatous, outer layers often dissociated, inner layers with starch grains. Endodermis: cells elliptical to polygonal. Stele usually dissected into 2–7 discrete vascular strands, each surrounded by endodermis and 3–6 arch. Stele medullated, undissected, 4–5 arch in some species of *Corybas*. Xylem tracheids mostly with helical or scalariform thickenings. Ergastic substances: raphides in ground tissue of *Acianthus* and *Corybas*; starch grains in all taxa.

Root

TRANSECTION

Hairs multiseriate, associated with mycorrhiza, in *Acianthus*, some species of *Corybas*, and *Townsonia*. Epidermis: cells elliptical to polygonal; walls of uniform thickness or outer wall thicker depending on taxon. Cortex parenchymatous, outer layers infected with hyphae and pelotons, inner layers often with starch grains. Endodermis: cells elliptical to polygonal. Stele medullated (sclerotic in *Cyrtostylis*), 3–10 arch. Xylem tracheids mostly with scalariform thickenings. Crystals: raphides in cortex.

Dropper/Root-like stolon

TRANSECTION

Hairs uniseriate, associated with mycorrhiza, in *Cyrtostylis* and *C. unguiculatus*, otherwise multiseriate. Epidermis: cells isodiametric to polygonal; walls of uniform thickness or outer wall thicker, depending on species. Cortex parenchymatous, outer layers infected with hyphae and pelotons, inner layers infrequently with starch grains. Endodermis: cells elliptical to polygonal. Stele medullated, 3–6 arch. Xylem tracheids mostly with scalariform or pitted thickenings. Crystals: raphides rare in cortex. **(AP)**

Phytochemistry

No phytochemical data have been reported in the literature for Acianthinae. **(NV, RG)**

Phylogenetics

Acianthinae was created by Schlechter to account for a group of terrestrial orchid genera in Polychondreae (= Neottieae) with small flowers in a few-flowered raceme, manifestly pedunculate, and a spurless labellum bare on the upper surface (Schlechter 1926). He grouped them together with Drakaeinae, Caladeniinae, and Corysanthinae, which was a reasonable assessment of their phylogeny. Dressler (1974, 1981, 1993) preferred to group Corysanthinae with the Acianthinae, based primarily on the results of a numerical analytical study by Lavarack (1971). Recent results of embryological (Clements 1995) and molecular analyses (Clements *et al.*, in preparation; Kores *et al.* 2000) have confirmed the presumed close relationship of Acianthinae to Corysanthinae, and secondly with Caladeniinae as a then sister group. **(MAC)**

Artificial key to the genera of Acianthinae (DJ)

1. • Flower solitary, with a very short peduncle and appearing to squat in the leaf base, dominated by the dorsal sepal and labellum; labellum base tubular with two closed spurs or cylindrical open-ended auricles; column completely enclosed within the labellum base . . . . **20. *Corybas***
   • Flowers 1–several, on a relatively long erect peduncle, not dominated by the dorsal sepal and labellum; labellum base never tubular and without spurs or auricles; column not enclosed within the labellum base 2

2 • Leaves one or two per tuber; column winged throughout . . . . **23. *Townsonia***
   • Leaf always one per tuber; column wings absent, vestigial or developed only near the column apex 3

3 • Labellum callus consisting of a large, entire or deeply lobed basal ridge . . . . **22. *Stigmatodactylus***
   • Labellum callus cushion-like or plate-like 4

4 • Pollinia attached to a viscidium; column wings absent or vestigial . . . . **19. *Acianthus***
   • Viscidium absent; column wings expanded distally . . . . **21. *Cyrtostylis***

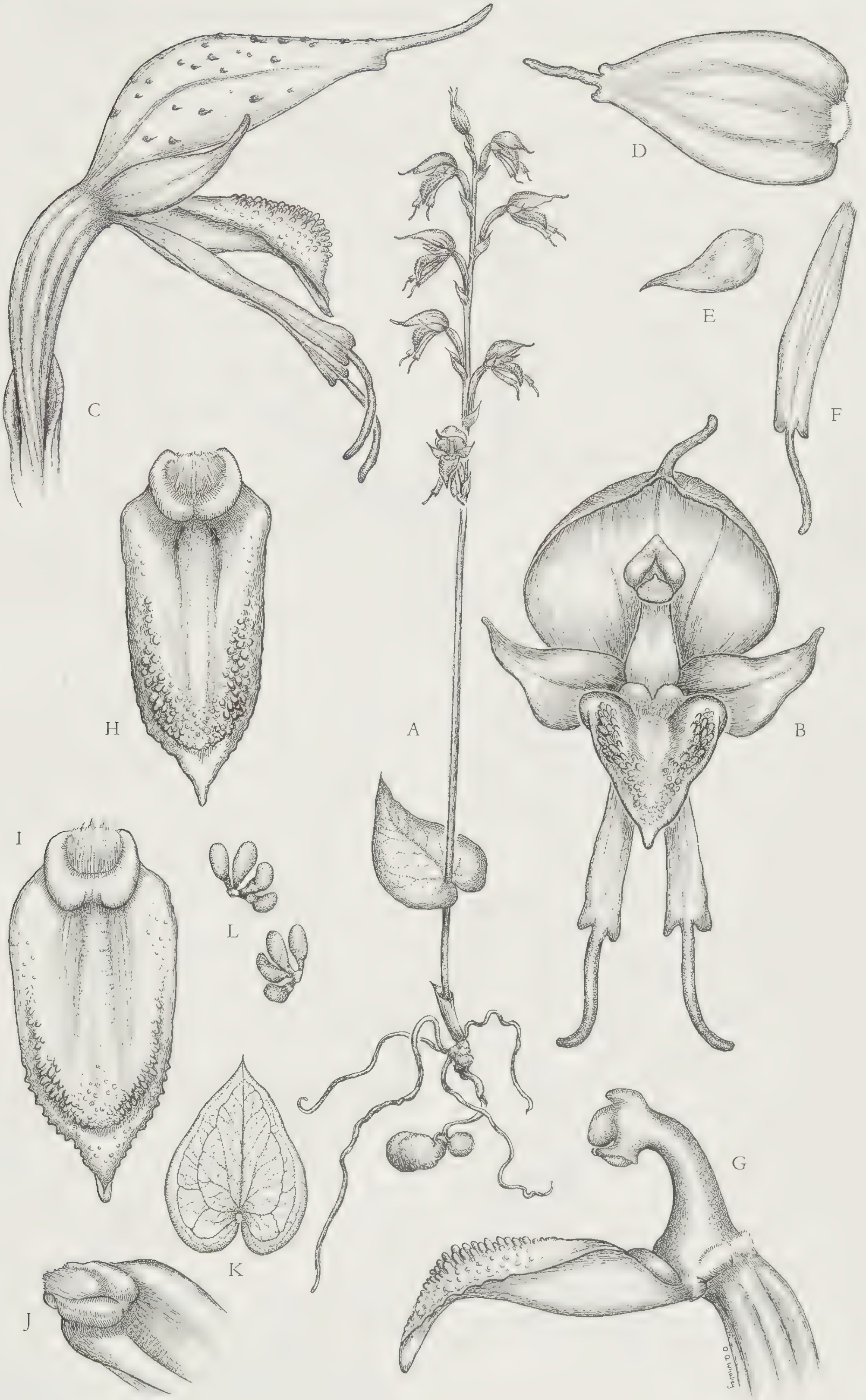

Fig. 19.1. *Acianthus fornicatus* R.Br. A. Habit, ×0.9; B. Flower from front, ×10.8; C. Flower from side, ×8.1; D. Dorsal sepal, ×5.4; E. Petal, ×5.4; F. Lateral sepal, ×5.4; G. Labellum and column from side, ×10.8; H. Labellum from above, ×10.8; I. Labellum from above, flattened, ×10.8; J. Basal gland of labellum, ×10.8; K. Leaf, ×0.9; L. Pollinarium, dissected ×18.9. Drawn by Oliver Q. Whalley from Kew Spirit Collection no. 37972.

19. ACIANTHUS

Acianthus R.Br., *Prodr.*, 321 (1810). Type species: *Acianthus exsertus* R.Br.

Derivation of name

From the Greek *akis*, point, and *anthos*, flower, referring to the slender apices of the sepals of some species. **(DJ)**

Description (Plate 13; Fig. 19.1)

Perennial geophytic *herbs*, sympodial. *Roots* absent. *Tubers* globose, paired, fleshy; replacement tubers formed at the end of short droppers; daughter tubers formed at the apex of root-like stolons subterranean axes with minute papillae each with apical unicellular hairs. *Stem* erect, short, unbranched, terete, with membranous cataphylls at each node. *Leaf* single, basal, in some species dimorphic between sterile and fertile plants; lamina membranaceous, held horizontally above the soil surface, flat, convolute in bud, sometimes lobed, abaxially with or without anthocyanin pigments; venation anastomosing, the main veins uniting apically; petiole fused with base of scape. *Inflorescence* racemose, one–several flowered, erect, terminal; scape lacking sterile bracts; floral bracts foliaceous, small. *Flowers* resupinate, small, dull-coloured, pedicellate. *Dorsal sepal* free, either much broader than lateral sepals or subsimilar, with or without a terete apical extension. *Lateral sepals* free, either much narrower than the dorsal sepal or subsimilar, with or without a terete apical extension. *Petals* free, either much smaller than the sepals or subsimilar. *Labellum* free, attached by its base to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina membranaceous, not lobed, flat or concave, margins flat or revolute, entire, denticulate or coarsely dentate, apex apiculate to acuminate; callus fleshy, either dominating most of the lamina or reduced to a central or basal plate, with or without two prostrate, tonsil-like basal glands and a narrow reticulate longitudinal channel; nectar present or absent. *Column* lacking free filament and style, slender, incurved near the apex; column wings fused throughout, vestigial or absent; column foot absent; anther terminal, two-celled, persistent, basifixed, porrect, rostrate or not; pollinarium present, consisting of four pollinia attached directly to a common viscidium or adjacent pairs attached to a hemiviscidium; pollinia subentire to strongly bilobed, waxy, yellow; pollen grains in tetrads; viscidium dorsal or terminal; rostellum ventral, transverse or two-lobed; stigma entire, small, concave. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, thin-walled, erect; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 19.2)

A genus of about 26 species distributed in mainland eastern Australia and Tasmania, New Zealand (including the Kermadec Islands, Chatham Islands, and Stewart Island), and New Caledonia (including Isle des Pins). **(DJ)**

Infrageneric treatment (DJ)

1. **Acianthus** subgenus **Acianthus** Kores, *Allertonia*, **7** (3), 148 (1995).
   - 1.1. **Acianthus** section **Acianthus** Kores, *Allertonia*, **7** (**3**), 198 (1995).
   - 1.2. **Acianthus** section **Caudatus** Kores, *Allertonia*, **7** (**3**), 194 (1995). Type species: *Acianthus caudatus* R.Br.
2. **Acianthus** subgenus **Univiscidiatus** Kores, *Allertonia*, **7** (**3**), 148 (1995).
   - 2.1. **Acianthus** section **Univiscidiatus** Kores, *Allertonia*, **7** (**3**), 163 (1995). Type species: *Acianthus elegans* Rchb.f.
   - 2.2. **Acianthus** section **Macropetalus** Kores, *Allertonia*, **7** (**3**), 149 (1995). Type species: *Acianthus cymbalariifolius* Rchb.f.

Palynology

The variously shaped pollen unit of *Acianthus fornicatus* R.Br (not recognizable as either monad or tetrad) is inaperturate, semitectate, reticulate, and suprabaculate-pilate (Ackerman and Williams 1981). **(AP)**

Ecology

Whereas the Australian and New Zealand taxa have been well studied, our knowledge of the ecology of many of the New Caledonian taxa is meagre. All species of *Acianthus* are terrestrial and grow as individuals or in loose groups and colonies. Eight of the ten Australian species, together with *A. sinclairii* Hook.f. from New Zealand, grow in robust clonal colonies, reproducing locally by means of daughter tubers formed on long root-like stolons. By contrast, *A. amplexicaulis* (Bailey) Rolfe, *A. sublestus* Dockrill from Australia, and the majority (if not all) of the species from New Caledonia reproduce solely from seed and grow as scattered individuals or in small, loose groups. All species of *Acianthus* are found in areas with seasonal climates and grow actively between February and August, flowering either as the leaves develop or well after they have matured. They are dormant during the extremes of heat or dryness, surviving as small fleshy tubers. Some species of *Acianthus*, such as *A. fornicatus* R. Br. and *A. sinclairii,* take 8–10 weeks to disperse seed after pollination, whereas in others, such as *A. amplexicaulis* and *A. elegans* R. Br., the lowermost capsules in an inflorescence may shed before the upper buds have opened.

Acianthus extends from about 20°–22° 30′ south in New Caledonia, between about 17°–43° south in Australia, and about 30°–47° south in New Zealand. Various species are distributed from sea level to montane areas at about 1100 m and without exception grow in mesic habitats. In Australia these habitats include sheltered slopes and gullies in rainforest, grassy to shrubby sclerophyll forest, woodland, and heathland. In New Zealand *A. sinclairii* grows mainly in lowland forest and scrub, often near tracks.

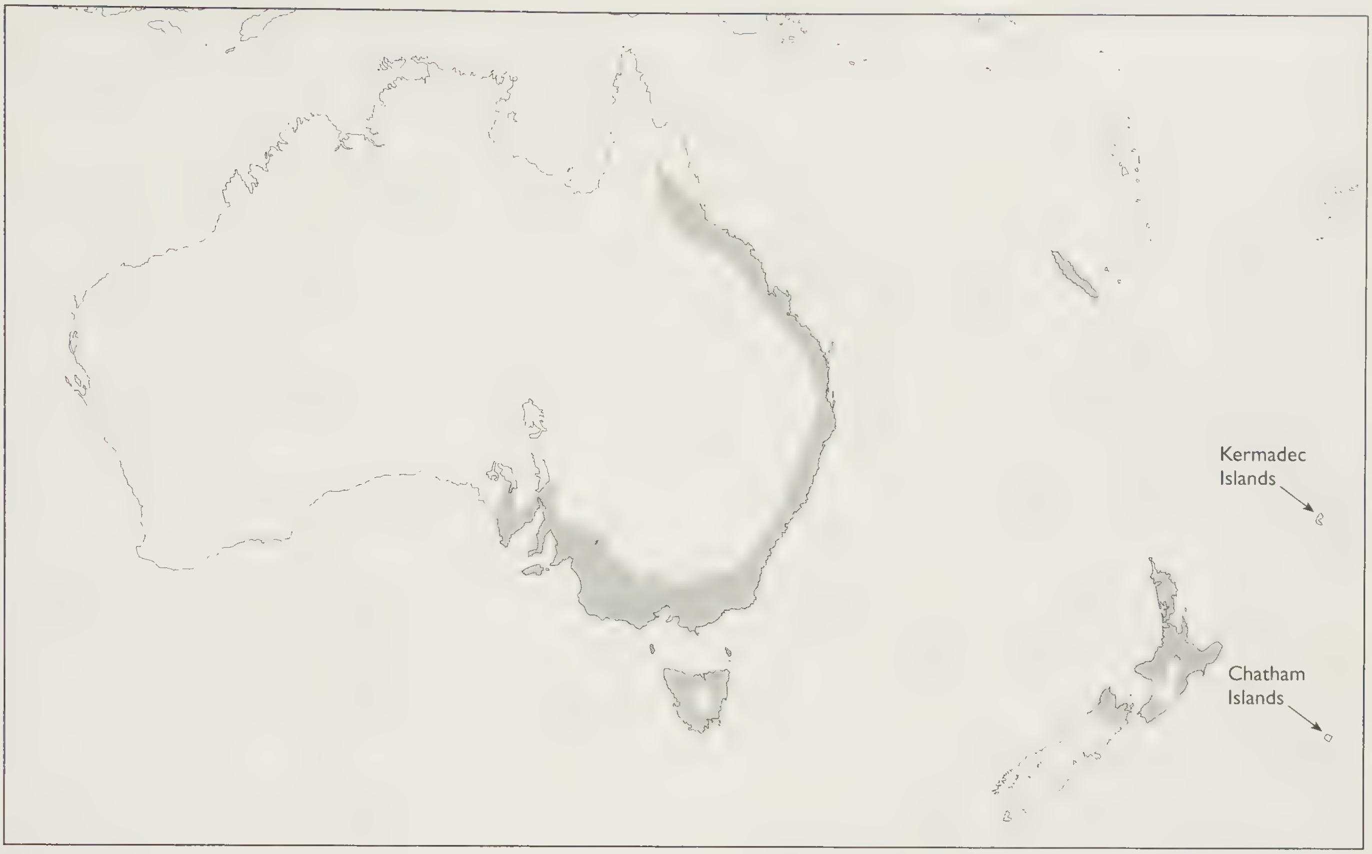

Fig. 19.2. Distribution map of *Acianthus*

Artificial key to the subgenera and sections of *Acianthus* (DJ)

1. • Viscidium 1; pollinia subentire, broadly ovate or obovate to suborbicular; dorsal sepal 1-nerved (very rarely 3-nerved) .... **2. *A.* subgenus *Univiscidiatus***
   • Viscidia 2; pollinia bilobed, more or less subreniform-falcate or subclavate; dorsal sepal 3–5-nerved ..... **3. *A.* subgenus *Acianthus***
2. • Petals reduced, 1-nerved; labellum base not hastate or sagittate; disc with a pair of basal calli; column not winged or appendaged .... **Section *Univiscidiatus***
   • Petals enlarged, 3–5-nerved; labellum base hastate or sagittate; disc with a single basal callus or naked; column winged and sometimes also with a prominent medial appendage .... **Section *Macropetalus***
3. • Sepals with terete apices; pollinia subclavate, waxy .... **Section *Acianthus***
   • Sepals long-acuminate-attenuate; pollinia subclavate, waxy .... **Section *Caudatus***

Habitats in New Caledonia include dense wet forests, rainforest, forest margins, maquis, gullies, and rocky shrubland, with the plants growing in soil, humus, moss carpets or on ultrabasic rocks. Most species grow in shady situations where the humidity is continually high or high at least during the growing season. **(DJ)**

Pollination

Most *Acianthus* species are pollinated by small delicate flies (Cheeseman 1875; Jones 1974, 1988) from families usually associated with rotting plant matter (Anisopodidae, Sciaridae) or fungi (Sciaridae, Mycetophilidae). Two species, *A. amplexicaulis* and *A. sublestus* Dockrill, are self-pollinating (Jones 1988).

Outcrossing *Acianthus* species provide nectar rewards for pollinators (Cheeseman 1875; Jones 1974). Most have little or no odour, except for *A. caudatus* R. Br. which emits a strong foul smell on warm days (Jones 1974; Bates and Weber 1990). In common with many myophilous species the flowers are inconspicuously coloured, often transparent pale white or light greenish with suffusions of brownish red. The labellum may be dark maroon and have areas of short black calli. Autogamous species tend to have little coloration.

Pollinators are actively attracted to both *A. sinclairii* (Cheeseman 1875) and *A. caudatus* (Jones 1974) on warm sunny days such that high levels of insect activity may be observed around large colonies of these plants. The pollination mechanism is similar in both species and likely to be representative of the genus. Typically, the *Acianthus* labellum has a shallow or deep depression forming a pool at the base for nectar secreted from two glands on the upper basal margin. In all cases the slender column arches over the nectar pool bringing the reproductive structures above its distal margin. Two pollinia lobes in each of the two terminal anther cells are attached directly to viscidia, one per anther cell. The viscidia are mounted on lobes of the rostellum that project from the upper margin of the stigma.

Flies attracted to *A. caudatus* move up the recurved labellum probing with the proboscis until they reach the nectar (Jones 1974). Imbibing the nectar involves a rhythmic up and down pumping action of the body. On upward movements the thorax may contact one or both of the downward projecting viscidia. When these adhere pollinia are withdrawn from the anther cells on downward movements. After feeding, flies become quiescent for a short period. Jones (1974) considered they may have been intoxicated or stupified by the nectar, allowing time for the viscidium to attach firmly to the thorax. However, the quiescence may simply be a resting period after feeding. Pollination occurs when flies bearing pollinia push them into the stigma during feeding movements.

The reward mechanism in *Acianthus* results in high levels of seed set (Cheeseman 1875; Jones 1974). Cheeseman (1875) reported that 71 seed capsules developed from 87 flowers (82%) on 14 plants of *A. sinclairii* at one location, whereas 44 out of 47 (94%) matured seed at another. Flowers failing to produce seed tended to be terminal buds that did not develop successfully.

There are no published details of the mechanism of autogamy in *A. amplexicaulis* and *A. sublestus*. Fitzgerald (1875) found that no seed developed when *A. fornicatus* and *A. exsertus* R.Br. flowers were isolated from insects by growing plants under a bell jar, indicating these species are not autogamous. Seed developed normally in *A. fornicatus* and *A. exsertus* if pollen was artificially placed on their stigmas (Fitzgerald 1875). **(CCB)**

Uses

The only use documented for *Acianthus* is as ornamentals by specialist growers. **(DJ)**

Cultivation

Many Australian species of *Acianthus* are successfully cultivated, such as *Acianthus apprimus* D. L. Jones, *A. pusillus* D. L. Jones, *A. exsertus*, and *A. fornicatus*. These are small-flowered terrestrials, insignificant on their own, but a pot full of 20 flowering plants makes a lovely display. Tubers should not be allowed to dry out too much over the dormant period.

Mix: basic, well drained. Light: 50% shade. Watering: Keep moist from late summer until late spring. Flowering: species in flower from early autumn until mid-winter. Propagation: Colony-formers, multiplication rate ×2 on average. **(HR)**

Taxonomic literature

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20. CORYBAS

Corybas Salisb., *Parad. Lond.*, t. 83 (1807). Type species: *Corybas aconitiflorus* Salisb.

Corysanthes R. Br., *Prodr.*, 328 (1810). Type species: *Corysanthes fimbriata* R. Br.

Calcearia Bl., *Bijdr.*, **6**, t. 1, fig. 3; **8**, 417 (1825). Type species: *Calcearia picta* Bl.

Corysanthes R. Br. sect. *Corybas* (Salisb.) Endl., *Gen. Pl.*, **1**, 218 (1837).

Corysanthes R. Br. sect. *Corysanthes* Endl., *Gen. Pl.*, **1**, 218 (1837).

Corysanthes R. Br. sect. *Steleocorys* Endl., *Gen. Pl.*, **1**, 218 (1837). Type species: *Corysanthes unguiculatus* R. Br.

Nematoceras Hook.f., *Fl. Nov. Zel.*, **1**, 249 (1853). Type species: not designated.

Corysanthes R. Br. sect. *Calcearia* (Blume) Schltr., *Repert. Spec. Nov. Regni Veg. Beih.*, **1**, 20 (1911).

Corysanthes R. Br. sect. *Gastrosiphon* Schltr., *Repert. Spec. Nov. Regni Veg. Beih.*, **1**, 20 (1911). Type species: *Corysanthes gastrosiphon* Schltr.

Corysanthes R. Br. sect. *Geosiphon* Schltr., *Repert. Spec. Nov. Regni Veg. Beih.*, **1**, 20 (1911). Type species: *Corysanthes saprophytica* Schltr.

Derivation of name

Referring to a corybant or dancing priest of the goddess Cybele in Phrygia. **(DJ)**

Description (Plates 14, 15; Fig. 20.1)

Perennial geophytic or epiphytic *herbs*. *Roots* absent. *Tubers* globose, paired, fleshy; replacement tubers formed at the end of short droppers; daughter tubers formed at the end of root-like stolons; subterranean axes with minute papillae each with apical unicellular hairs. *Stem* erect, short, unbranched, terete, with membranous cataphylls at each node. *Leaf* single, basal; lamina membranaceous, epigeous, flat, convolute in bud, hypostomatic, abaxially pellucid or with anthocyanin; venation anastomosing, the main veins uniting apically. *Inflorescence* one-flowered, terminal; peduncle lacking sterile bracts; floral bracts foliaceous, small. *Flowers* resupinate, small, fungiform, dull-coloured, shortly pedicellate. *Dorsal sepal* free, much larger than the lateral sepals, usually cucullate. *Lateral sepals* free, much smaller than the dorsal sepal, often basally auriculate. *Petals* free, subsimilar to the lateral sepals or even smaller. *Labellum* free, attached by its base to the anterior column base, markedly dissimilar in size and shape to the sepals and petals; lamina membranaceous, not lobed, tubular in the erect proximal part then recurved, the distal part tubular or expanded, folded or thickened along the midline, the anterior surface smooth or papillate, margins incurved or flat, entire, crenate, denticulate or dentate; labellum base with a pair of open folded auricles or closed spurs; callus consisting of either overlapping plates in the tubular lip base or of acicular moniliform cells clustered along a thickened midline; nectar absent. *Column* lacking free filament and style, slender to squat, straight or incurved near the apex; column wings mostly fused to the column, the tips free; column base with or without lateral auricles, the anterior base often expanded into a swollen, fleshy, red mound; column foot absent; anther terminal, two-celled, persistent, basifixed, erect, not rostrate; pollinarium present, consisting of four pollinia attached directly to a viscidium; pollinia unequal, mealy, cream; pollen grains in monads or tetrads, viscidium dorsal; rostellum dorsal, transverse; stigma entire, concave. *Ovary* elongate, often recurved, ribbed, glabrous. *Capsules* dehiscent, thin-walled, raised on an elongate and thickened peduncle. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 20.2)

A genus of about 120 species distributed in India, South China, Taiwan, peninsular Malaysia, Borneo, Philippines, New Caledonia, Vanuatu, Ponape, Indonesia, New Guinea, Solomon Islands, Australia (including Macquarie Island), New Zealand (including Chatham Islands, Stewart Island, Auckland Islands, and Campbell Island), Tahiti, Samoa, and Society Islands. **(DJ)**

Infrageneric treatment (DJ)

1. **Corybas** section **Corybas** P. Royen, *Phanerogamarum Monographiae Tomus*, **16**, 19 (1983).

Corysanthes R. Br. section *Corysanthes*; Endl., *Gen. Pl.*, 218 (1837).

Corysanthes R. Br. section *Geosiphon* Schltr., *Rep. Spec. Nov. Regni. Veg., Beih.*, **1**, 25 (1921). Type species: *Corysanthes saprophytica* Schltr.

1.1. **Corybas** subsection **Corybas** P. Royen, *Phanerogamarum Monographiae Tomus*, **16**, 19 (1983).

Corysanthes section *Calcearia* (Bl.) Schltr. Type species: *Corysanthes picta* (Bl.) Lindl.

1.2. **Corybas** subsection **Gastrosiphon** (Schltr.) P. Royen, *Phanerogamarum Monographiae Tomus*, **16**, 19 (1983). Type species: *C. gastrosiphon* (Schltr.) Schltr.

Corysanthes R. Br. section *Gastrosiphon* Schltr., *Rep. Spec. Nov. Regni. Veg., Beih.*,**1**, 18 (1914). Type species: *Corysanthes gastrosiphon* Schltr.

2. **Corybas** section **Steleocorys** (Endl.) P. Royen, *Phanerogamarum Monographiae Tomus*, **16**, 20 (1983). Type species: *C. unguiculatus* (R. Br.) Rchb.f.

Corysanthes R. Br. section *Steleocorys* Endl., *Gen. Pl.*, 218 (1837).

Corybas Salisb. section *Auriculata* P. Royen, *Alp. Fl. New Guinea*, **2**, 69 (1978). Type species: *C. unguiculatus* (R. Br.) Rchb.f.

Palynology

Monads of *Corybas aconitiflorus* Salisb. are globose-spherical, *c.* 15 μm, apolar, radiosymmetrical, inaperturate, semitectate, rugulate or rugulate-baculate, with a scabrate nexine (Ackerman and Williams 1981). **(AP)**

Ecology

Specimens of *Corybas* are infrequently collected because of their reduced habit, inconspicuous and fleeting flowers, and cryptic nature. Consequently, they have been inadequately studied in many regions. As pointed out by Dransfield *et al.* (1986), differentiating characters obvious in fresh material are lost when specimens are dried or stored in spirit. This makes herbarium interpretation difficult and reinforces the importance of field studies.

Artificial key to the sections and subsections of *Corybas* (DJ)

1. • Labellum base with two open auricles or slits . . . . Section ***Steleocorys***
   • Labellum base with two closed spurs . . . . **Section *Corybas* (2)**

2. • Ventral part of labellum not swollen . . . . Subsection ***Corybas***
   • Ventral part of labellum prominently swollen . . . . Subsection ***Gastrosiphon***

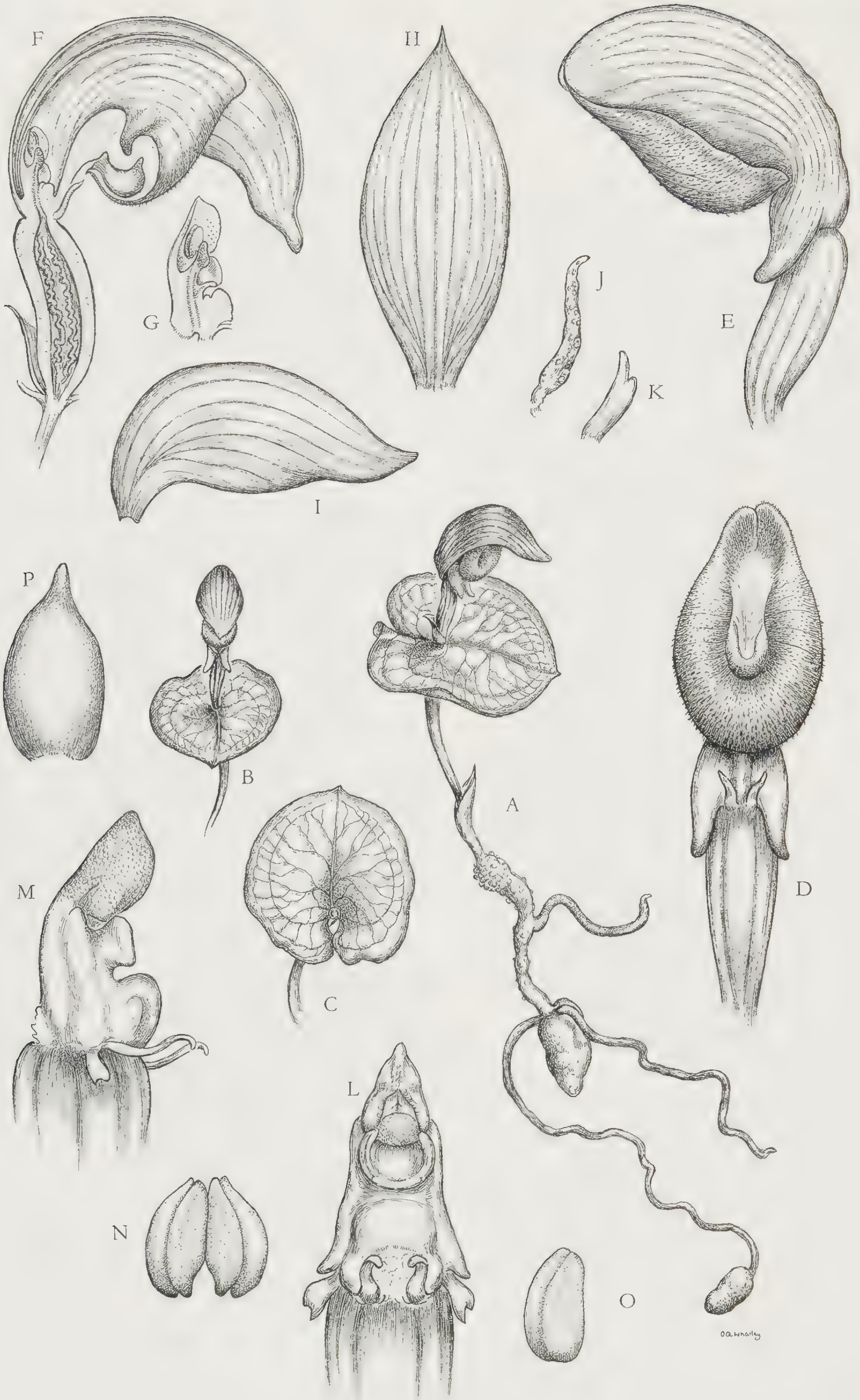

Fig. 20.1. *Corybas aconitiflorus* Salisb. A. Habit, ×1; B. Inflorescence from front, ×1; C. Leaf from above, ×1; D. Labellum with basal spurs and ovary from front, ×4.5; E. Labellum and ovary from side, ×4.5; F. Flower, longitudinal section, ×3; G. Column, longitudinal section, ×9; H. Dorsal sepal, ×3; I. Dorsal sepal from side, ×3; J. Lateral sepal, ×21; K. Petal, ×21; L. Column with lateral sepals and petals from front, ×15; M. Column with lateral sepals and petals from side, ×15; N. Pollinarium, ×21; O. Pollinarium from side, ×21; P. Floral bract, ×6. Drawn by Oliver Q. Whalley from Kew Spirit Collection nos. 37976 and 37831.

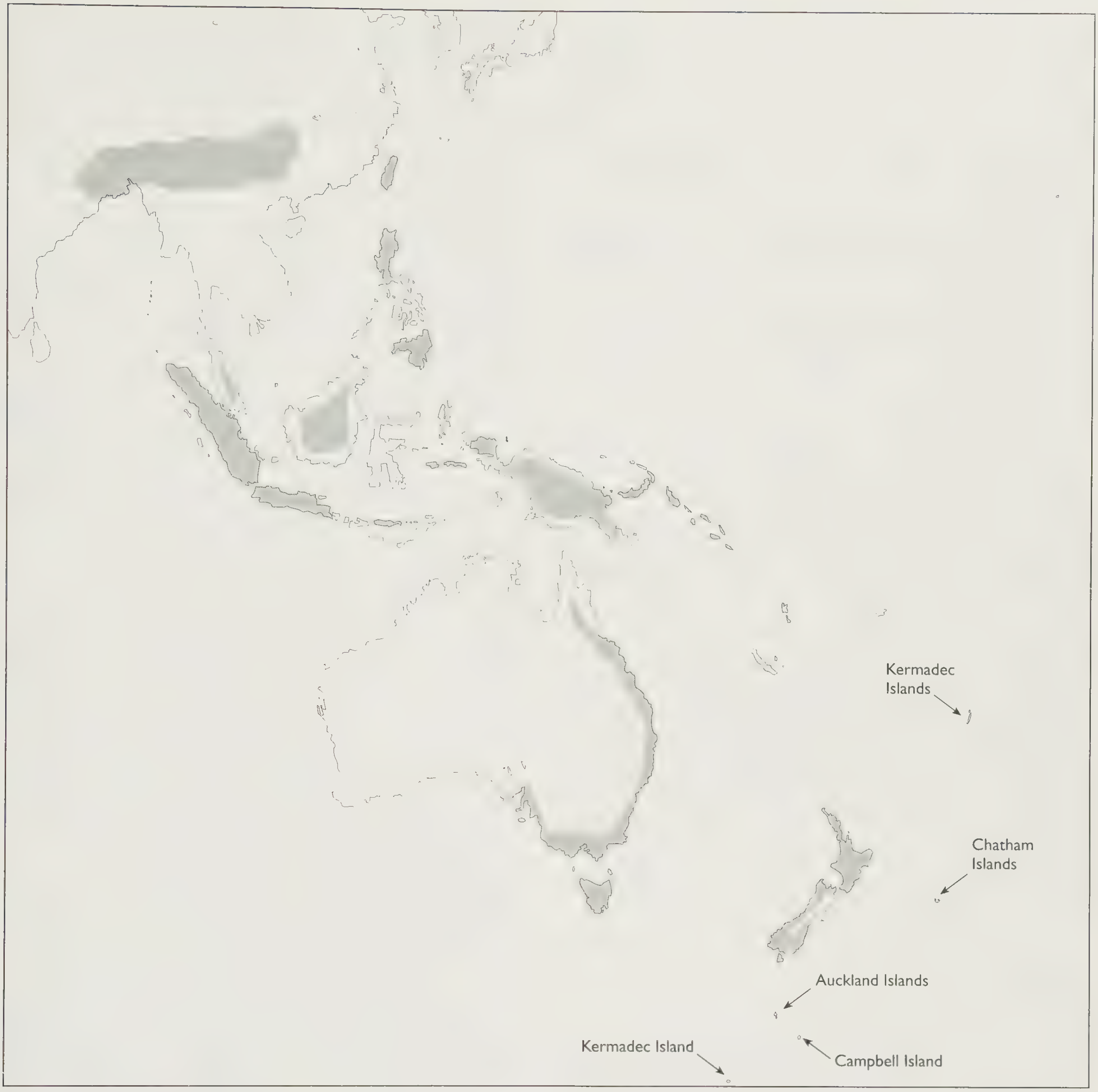

Fig. 20.2. Distribution map of *Corybas* (partial range; see text).

Corybas species grow either as terrestrials in soil or humus or epiphytically in the fibrous trunks of tree ferns or on the mossy trunks, boles, and larger branches of trees. Many species form clonal colonies, but it is not known whether this is a character shared by all species because many of the tropical ones grow widely spaced in small groups. Species from tropical regions are markedly influenced by the monsoons, whereas those from temperate regions occur in areas with seasonal climates and grow mainly between March and August. They are dormant over summer, surviving as small fleshy tubers and avoiding the extremes of heat, low humidity, and dryness.

Flowering in *Corybas* from temperate regions occurs from autumn to spring, whereas in the tropics the response is more complex and less studied. Some tropical species, especially those from low to mid-elevations, are tied in closely to the wet season, but others from higher elevations appear to have a defined flowering period. Elongation and thickening of the peduncle prior to seed shedding can be dramatic in some species (as much as 30 cm in *C. incurvus* D. L. Jones & M. A. Clem.) and much less obvious in others such as *C. unguiculatus* (R.Br.) Rchb.f. It is unknown whether all species of *Corybas* have this habit. The period from pollination to seed shedding is about 8–10 weeks in species from temperate regions but is probably much shorter in those from the tropics.

Species of *Corybas* are distributed from the tropics to subantarctic islands and occupy a wide range of mesic habitats from the lowlands to montane and alpine zones. They are found over an extensive latitudinal range, extending from southern China (about 22° north) to Macquarie Island (about 54° south). The centre of proliferation for *Corybas* is New Guinea where there are about 50 species, with some recorded from the lowlands but the majority occurring at higher elevations in montane forests and grasslands. About eight species are known from the higher mountains above 2750 m, growing in subalpine and alpine zones. *Corybas aundensis* P. Royen has been collected from about 3600 m in the Lake Aunde–Mt. Otto region. The habitats in such regions include moss cushions in densely shaded wet forests, shrubbery, mixed conifer forests, and moss forests (van Royen 1979).

In New Guinea, western Malesia, and Asia, collections have been made from a wide range of habitats including *Imperata* Cyrilli grassland in partial shade or full sun; in moss and among humus and leaf litter on mountain ridges, particularly in moss forests; among litter in moist dark forests; epiphytic on the mossy boles of large trees and low branches; mossy banks in 'kerangas' forest; in sphagnum mounds and bogs; and thin soil and moss carpets on serpentine. Australian habitats are similarly varied and include fern gullies, where the orchids can grow as terrestrials in moist to wet soil or epiphytic on the trunks of the tree fern *Dicksonia antarctica*; sheltered slopes in sclerophyll forest and woodland; rainforest margins; heathland; coastal scrub on consolidated dunes; mallee shrubland over limestone; and on hummocks in moist to wet swamps. In New Zealand *Corybas* plants are found in a variety of open to dense, moist forests and often colonize shady embankments. The habitat of *C. dienemus* D. L. Jones on Macquarie Island is bleak, windswept beach terraces. In New Caledonia *Corybas* grow in rainforest and sheltered maquis on ultrabasic soils, from low montane areas to mountain tops at about 1250 m. **(DJ)**

Pollination

Little is known about the pollination of *Corybas* species, partly because the flowers are inconspicuous and partly because the column is hidden deep within an opaque tube formed by the labellum and dorsal sepal. The latter means it is impossible to observe pollinator behaviour within the flower, so the mechanism can only be inferred from flower structure and the position of pollinia on the insect.

Only two insect specimens associated with *Corybas* flowers have been formally identified. Both were fungus gnats of the family Mycetophilidae. Miller (1918) described a new species of mycetophilid, *Exechia thomsonii*, that had been found by G. M. Thomson in a flower of *Corybas oblongus* Rchb.f. (recorded as *Corysanthes oblonga* Hook.f.) with pollinia on its thorax. Thomson (1879) had previously reported the occurrence of 'small Diptera—probably a species of *Culex*' in flowers of *Corybas macranthus* (Hook.f.) Rchb.f. (recorded as *Corysanthes macrantha* (Hook.f.) Hook.f.) with pollinia 'attached to the front of the head'. It is likely the '*Culex*' in reality were mycetophilids since mosquitoes and fungus gnats are similar in general appearance, particularly in the humped thorax, which Thomson appears to have mistaken for the head region. The second confirmed report of a mycetophilid associated with *Corybas* is of a single specimen found dead by Jones (1970*b*) on the labellum of a flower of *C. incurvus* D. L. Jones & M. A. Clem. (recorded as *C. diemenicus* (Lindl.) Rchb.f.). The gnat specimen was not identified beyond family but bore pollinia identical to those of *C. incurvus* on the dorsal anterior of its thorax.

The limited data indicate *Corybas* species may be pollinated primarily by mycetophilids and are therefore sapromyophilous. The floral characteristics of *Corybas* certainly conform with sapromyophily. The flowers are inconspicuous, dull-coloured with shades of reddish or brownish purple, and lack a sweet odour. No odours have been reported from *Corybas* species, although Jones (1970*b*) proposed that they may be present but undetectable by humans. Sapromyophilous flowers often have slits or holes in the side (van der Pijl and Dodson 1966), which may represent the auricles found at the base of the labellum in species of section *Steleocorys*. Jones (1970*b*) hypothesized that these may allow the movement of air into the base of the floral tube to aid in the dispersal of attractive odours.

Nectar or other food is usually absent from sapromyophilous flowers, and there are no reliable reports of food rewards in *Corybas* species. Thomson (1879) noted that *C. macranthus* does not secrete any nectar, but that if the labellum is punctured copious amounts of a 'sweetish purple juice exudes' which may be taken by insects. Similarly, Coleman (1931*a*) noted that the base of the column is swollen in *C. aconitiflorus* Salisb. (recorded as *Corysanthes bicalcarata* R. Br.) and found that liquid oozes out when it is punctured with a needle, implying that it might be a source of nectar. Jones (1970*b*) rejected Coleman's (1931*a*) hypothesis of a basal nectar gland on the column, noting that liquid oozes from any punctured surface on the column and is probably not nectar. Jones (1970*b*) drew attention to two small glands on either side of the column base in *C. incurvus* which he supposed may be nectaries or scent glands. If they are scent glands, their location near the auricles may facilitate odour dispersion.

A further characteristic of many sapromyophilous flowers is the presence of long filiform tails on the floral segments. These tails are found in diverse fly-pollinated groups including orchids such as many *Bulbophyllum* and *Pterostylis*. The function of the tails is not known, but they may guide flies to the labellum (van der Pijl and Dodson 1966). Many *Corybas* species have long, filamentous lateral sepals and petals, particularly those of New Zealand (Johns and Molloy 1983) and various Asian and Malesian species (Dransfield *et al.* 1986). Curiously, this feature is not found in any Australian species.

The column in most *Corybas* species is short and lies more or less horizontally between the bases of the labellum and dorsal sepal. The position of the pollinia on the thorax indicates that gnats land on the labellum, enter the floral tube and walk to the bottom, possibly attracted by the glands at the base of the column identified by Jones (1970*b*). Close investigation of the glands with the mouthparts or antennae would bring the thorax into contact with the stigma allowing deposition of incoming pollinia. This would be enabled by the peculiar structure of most mycetophilids in which the head is bent below the thorax in front of the forelegs. Slight upward movement of the thorax would bring it into contact with the single sticky viscidium on the rostellum to which the four pollinia are directly attached. Retreat of the gnat backwards would result in removal of the pollinarium on the thorax. The highly confined space in the floral tube indicates gnats would have to back out to escape (Thomson 1879).

Thomson (1879) found that pollinators of *C. macranthus* sometimes became stuck in the flower and may die or be consumed by spiders. He proposed that the flies adhered to the stigma and/or were unable to move backwards. When such flies were pulled out, the pollinarium came away with them, attached to the front of the head (*sic*). Trapped insects were found in six out of 145 flowers (Thomson 1879). Jones (1970a) noted that the labellum of *C. diemenicus* is armed with downward-pointing spines on the inner surface of the floral tube. These may function to prevent the easy retreat of gnats and ensure they proceed to the base of the tube. However, it may also mean some gnats are unable to escape.

Only a small proportion of *Corybas* flowers appear to set seed except in autogamous species. Thomson (1879) noted that 90 flowers of *C. macranthus* out of 145 had pollinia removed, but only a few set seed. Coleman (1933a) also noted that even though the pollinia had been removed from about 50% of *C. aconitiflorus* flowers only 1% were pollinated. The low rate of pollination and seed set may be related to the deceptive strategy adopted by *Corybas* species. This contrasts with reward-offering genera such as *Acianthus* in which seed set is often high. It may be that flies rapidly learn to avoid food-deceptive orchids.

According to Molloy (1990) four species of *Corybas* in New Zealand are autogamous, including *C. oblongus*. However, the mycetophilid pollinator described by Miller (1918) was collected from a *C. oblongus* flower. It is possible that *C. oblongus* is only facultatively autogamous or that some populations differ in their pollination strategies. Molloy (1990) provides no details of the mechanisms of autogamy for the species he nominated, although Hatch (1952) gave some information for *C. cryptanthus* Hatch (recorded as *C. saprophyticus* Hatch). In common with most autogamous species all flowers of *C. cryptanthus* set seed. Self-pollination occurs when the pollinia fall from the anthers onto the stigma. **(CCB)**

Uses

The only use documented for *Corybas* is as ornamentals by specialist growers. **(DJ)**

Cultivation

Many species from temperate areas of Australia grow well in cultivation (*C. aequalis* D. L. Jones, *C. aconitiflorus*, *C. fimbriatus* (R.Br.) Rchb.f., *C. pruinosus* (A. Cunn.) Rchb.f., *C. recurvus*), but others (*C. unguiculatus*, *C. undulatus* (A. Cunn.) Rupp, *C. fordhamii* (Rupp) Rupp) have not been maintained in cultivation for a long time. Those that grow successfully will respond well to the following conditions. Species generally occur in areas of higher humidity and therefore can be grown successfully in the more humid environment of a glasshouse. Tubers are more prone to desiccation over summer; therefore do not allow potting mixes to become too dry for too long.

Mix: basic mix with extra leaf mould added (as they frequently grow in damper areas where extra leaf litter accumulates). Light: 60–70% shade. Watering: keep moist from late summer until late spring. Flowering: Flowers are susceptible to desiccation and subsequent collapse from the early bud stage. Maintain humidity around developing flowering plants by either placing the plant in a plastic dome, a larger pot for protection or in the more humid atmosphere of a glasshouse. Propagation: colony-formers, multiplication rate ×2 on average. **(HR)**

Taxonomic literature

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21. CYRTOSTYLIS

Cyrtostylis R. Br., *Prodr.*, 322 (1810). Type species: *Cyrtostylis reniformis* R. Br.

Acianthus subgenus *Acianthus* section *Cyrtostylis* (R. Br.) Kores, *Allertonia*, **7**, 181 (1995).

Derivation of name

From the Greek *kyrtos*, curved, and *stylos*, pillar, column, referring to the curved column found in these orchids. **(DJ)**

Description (Plate 16; Fig. 21.1)

Perennial, geophytic *herbs*. *Roots* absent. *Stem* terete. *Tubers* globose, paired, fleshy; replacement tubers formed at the end of short droppers; daughter tubers formed at the end of root-like stolons; subterranean axes with minute papillae each with apical unicellular hairs. *Stem* erect, short, unbranched, terete, with membranous cataphylls at each node. *Leaf* single, basal; lamina membranaceous, epigeous, flat, convolute in bud, pellucid abaxially; venation anastomosing, the main veins uniting apically. *Inflorescence* racemose, one–several flowered, erect, terminal; scape lacking sterile bracts; floral bracts foliaceous, small. *Flowers* resupinate, small, dull-coloured, pedicellate. *Dorsal sepal* free, broader than the lateral sepals. *Lateral sepals* free, narrower than the dorsal sepal. *Petals* free, subsimilar to the lateral sepals. *Labellum* free, attached by its base to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina membranaceous, not lobed, flat, margins flat, entire or denticulate, apex apiculate; callus a narrow central raised plate extending nearly to the labellum apex, with two erect basal glands each with a dark terminal spot; nectar present. *Column* lacking free filament and style, slender, incurved near the apex; column wings fused to the column, vestigial; column foot absent; anther terminal, two-celled, persistent, basifixed, porrect, not rostrate; pollinarium absent; pollinia four, strongly and unequally bilobed, mealy, yellow; pollen grains in tetrads; viscidium absent; rostellum ventral, transverse; stigma entire, small, concave. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, thin-walled, erect; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 21.2)

A genus of six species distributed in Australia and New Zealand. **(DJ)**

Palynology

Nothing has been published about pollen ultrastructure of *Cyrtostylis*. **(AP)**

Ecology

Species of *Cyrtostylis* are terrestrial and grow in clonal colonies reproducing locally by means of daughter tubers formed on slender stolonoid roots. All species are found in areas with seasonal climates and grow actively between March and September, flowering long after the leaves have matured. The period between pollination and seed dispersal is about six to eight weeks. Plants die down over summer to small fleshy tubers that are dormant during the extremes of heat or dryness.

Latitudinally *Cyrtostylis* extends from about 27° south to about 43° south. They are mainly orchids of lowland areas and without exception grow in mesic habitats. The Australian species occur in gullies and on sheltered slopes in sclerophyll forest, heathland, mallee shrubland over calcareous sand or limestone, and coastal scrub on stabilized dunes. The New Zealand species occupy light forest and scrubs, often colonizing track verges and embankments. **(DJ)**

Pollination

The many similarities in flower structure between *Cyrtostylis* and *Acianthus* led Cheeseman (1875) to suggest that the pollination mechanisms of the two genera are similar. As with *Acianthus*, *Cyrtostylis* may be myophilous, but there is little information on the pollinators. However, like *Acianthus*, the flowers of *Cyrtostylis* exhibit few of the characters typical of sapromyophily. Although they are inconspicuous and reddish brown in colour, they lack any obvious foul odour, trap-like structures, filiform tails, or vibrating frills normally associated with sapromyophily (van der Pijl and Dodson 1966). Unlike many sapromyophilous genera, *Acianthus* and *Cyrtostylis* offer food as a reward.

By contrast to *Acianthus*, the labellum of *Cyrtostylis* is flat and angled slightly below the horizontal to allow droplets of nectar to run down the middle (Cheeseman 1875). The column is arched over the centre of the labellum in a similar manner to *Acianthus*. A significant difference is the presence of column wings in *Cyrtostylis* to assist in orientation of the pollinator (Cheeseman 1875) in the absence of the nectar pool that positions them in *Acianthus*.

According to Cheeseman (1875), nectar in *C. oblonga* is secreted by a pair of raised glands at the base of the labellum, which are the homologues of similar glands in *Acianthus*. Droplets of nectar run down either side of the narrow, central callus plate extending to the tip of the labellum. On the other hand, Erickson (1965) found that nectar ran down the grooved centre of the callus plate in *C. huegelii* Endl. She also suggested that the nectar arose from a small well at the broader base of the callus plate in young flowers but that it disappeared in older flowers. She overlooked the role of the basal glands and may have mistaken a temporary depression in the labellum of unfolding flowers for a secretory gland.

Erickson (1965) surmised that an insect visiting the flowers of *C. huegelii* would land on the labellum and follow the nectar trail to the base. This would align it lengthwise along the labellum so that its thorax would pass between the column wings, allowing pollination to occur. The column of *Cyrtostylis* is similar to that of *Acianthus* except there is no distinct viscidium, but rather the rostellum secretes a copious coating of viscid fluid over the lower parts of the pollinia (Erickson 1965; Jones and Clements 1987).

There are no published descriptions of pollination in *Cyrtostylis* and no reports of identified pollinators. Cheeseman (1875) noted that *C. oblonga* Hook.f. was commonly visited by insects, chiefly minute species of Diptera, but these were not identified. Plate 17 is a previously unpublished photograph of a fly bearing pollinia and feeding on the labellum of *C. reniformis* R. Br. The fly is an undescribed species of *Atrichopleura* (Empididae) identified by D. K. McAlpine and lodged at the Australian Museum, Sydney. The fly was observed on the flower for about 45 minutes in September 1988 near Eugowra in New South Wales (C. C. Bower, unpublished). During most of this time it appeared to feed near the base of the labellum with its thorax between the column wings. The pollinarium was placed centrally near the rear of its thorax and for most of the observation period was in contact with the stigma.

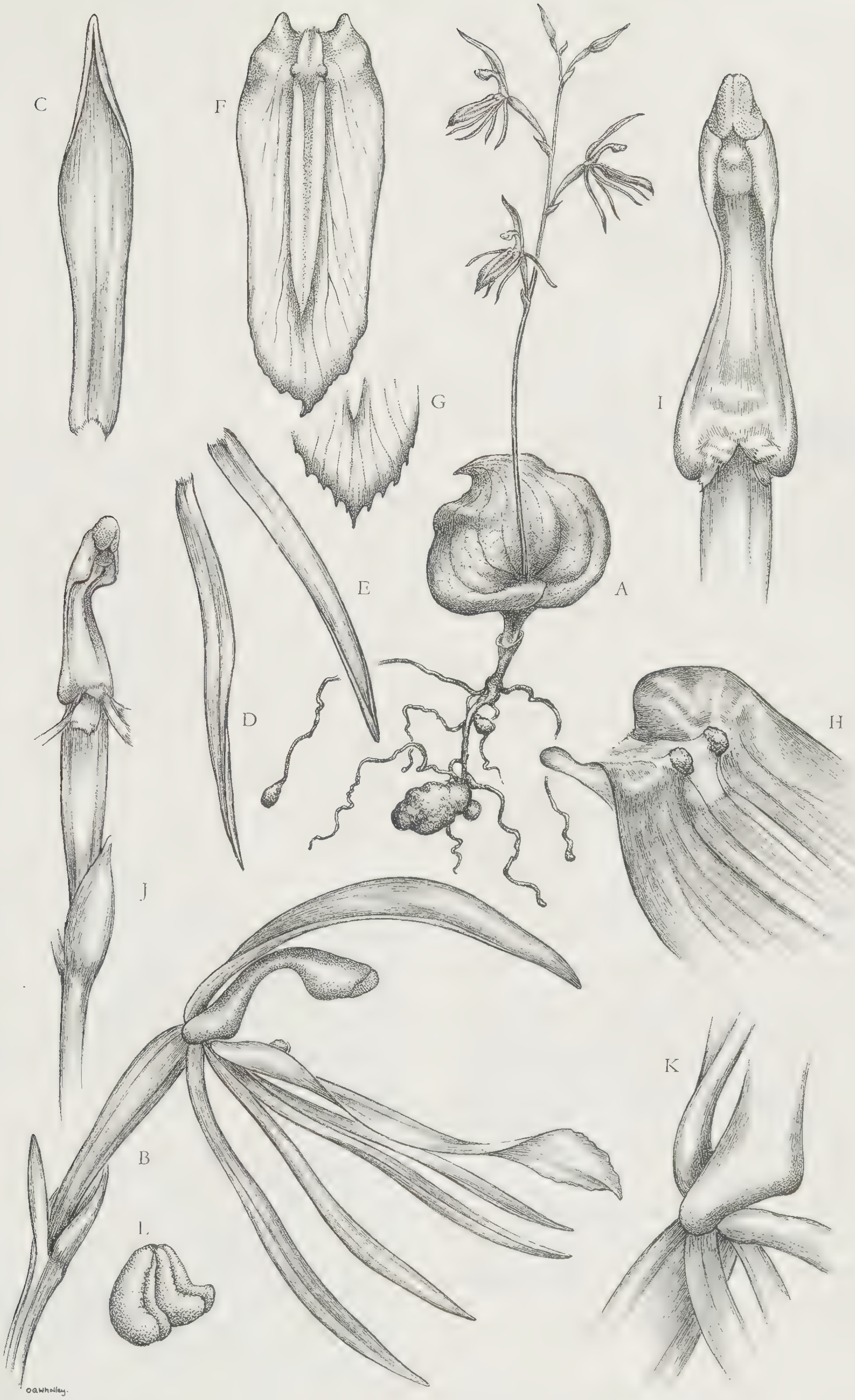

Fig. 21.1. *Cyrtostylis reniformis* R.Br. A. Habit, ×0.9; B. Flower from side, ×5.4; C. Dorsal sepal, ×5.4; D. Lateral sepal, ×5.4; E. Petal, ×5.4; F. Labellum, ×5.4; G. Labellum apex, variation, ×5.4; H. Labellum base, showing nectar glands, ×13.5; I. Column from front, ×10.8; J. Column and ovary with bract (perianth removed), ×5.4; K. Enlargement of articulation between column and labellum base (with the bases of some perianth parts), ×13.5; L. Pollinia, ×18.9. Drawn by Oliver Q. Whalley from *Williamson 48* (K) and Kew Spirit Collection no. 55553.

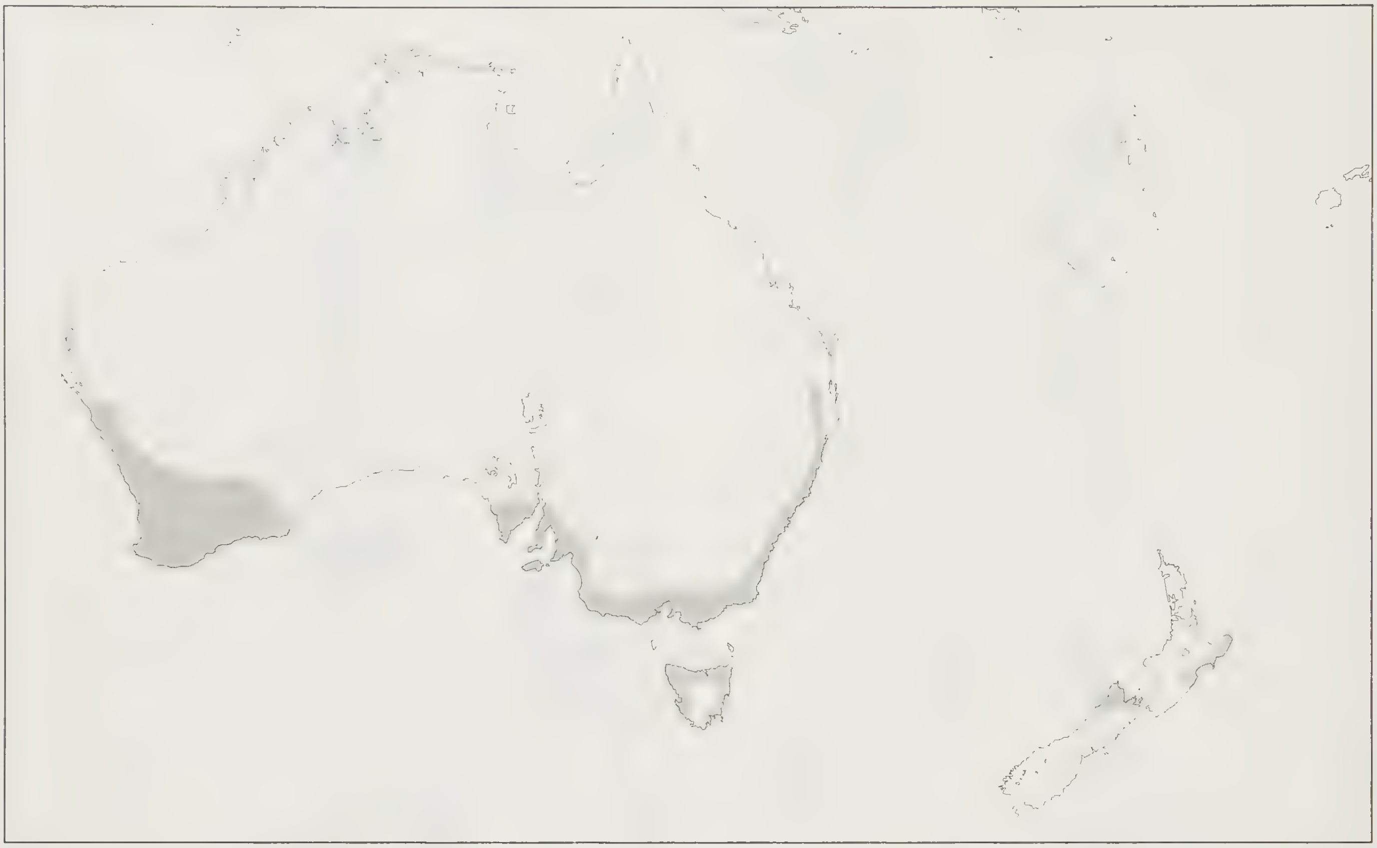

Fig. 21.2. Distribution map of *Cyrtostylis*.

Twice the fly made excursions down the labellum, apparently feeding on nectar in the grooved callus plate before returning to its original position. Finally it moved to the top of the column where it tried to remove the pollinia with its legs before being captured. Once in the specimen tube the fly became active but until then had been rather sluggish. The movements of the fly on the labellum indicate that self-pollination could easily occur during second or third bouts of feeding. The fly did not undergo the rhythmical up and down movements during feeding reported by Jones (1974) for the fly pollinators of *Acianthus caudatus*.

Empidid flies are considered to be predatory on smaller insects and not attracted by dead or rotting matter (Colless and McAlpine 1991). If such flies are the normal pollinators it would appear that *Cyrtostylis* is myophilous. **(CCB)**

Uses

The only use documented for *Cyrtostylis* is as ornamentals by specialist growers. **(DJ)**

Cultivation

All species except *C. tenuissima* (Nicholls & Goadby) D. L. Jones & M. A. Clem. respond well in cultivation. Individual flowers are easily overlooked, but a group of flowering plants looks like a swarm of hovering insects. Tubers should not be allowed to dry out excessively over summer.

Mix: basic, well drained. Light: 50% shade. Watering: keep moist from late summer until late spring. Flowering: species in flower from winter to late spring. Propagation: colony-formers, with multiplication rate ×2 on average. **(HR)**

Taxonomic literature

Johns, J. and Molloy, B. (1983). *Native orchids of New Zealand.* A. H. & A. W. Reed, Wellington.

Jones, D. L. (1998). Contributions to Tasmanian orchidology—1: introduction and the genera *Acianthus, Arthrochilus, ×Calassodia, Calochilus, Corybas, Cyrtostylis, Dipodium, Dockrillia, Gastrodia, Leptoceras, Microtis, Pyrorchis* and *Townsonia. Australian Orchid Research*, **3**, 1–15.

Jones, D. L. and Clements, M. A. (1987). Reinstatement of the genus *Cyrtostylis* R. Br. and its relationships with *Acianthus* R. Br. (Orchidaceae). *Lindleyana*, **2**, 156–60.

Kores, P. J. (1995). A systematic study of the genus *Acianthus* (Orchidaceae: Diurideae). *Allertonia*, **7**, 87–220.

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22. STIGMATODACTYLUS

Stigmatodactylus Maxim. ex Makino, *Illustr. Fl. Jap.*, **1(7)**, 11 (1891). Type species: *Stigmatodactylus sikokianus* Maxim. ex Makino.

Pantlingia Prain, *J. Asiatic. Soc. Bengal*, **65**, 106–9 (1896). Type species: *Pantlingia paradoxa* Prain.

Derivation of name

From the Greek *stigma*, *stigmatos*, mark or spot (but interpreted botanically as a stigma), and *daktylos*, finger, in reference to a dactyliform appendage on the lower stigma margin in these orchids. **(DJ)**

Description (Plate 18; Fig. 22.1)

Perennial geophytic *herbs*. *Roots* absent. *Tubers* in most species globose, tiny, solitary, fleshy (elongate and rhizomatous in *S. paradoxus* Schltr.); replacement tubers formed at the end of short droppers (except in *S. paradoxus*); daughter tubers absent or lateral on root-like stolons; subterranean axes with minute papillae, each with apical unicellular hairs. *Stem* erect, short, unbranched, terete or four-angled, with membranous cataphylls at each node. *Leaf* single, cauline (reduced to a sheathing bract in *S. paradoxus*); lamina membranaceous, held well above the soil surface, flat, convolute in bud, margins entire or crispate; venation anastomosing, the main veins uniting apically. *Inflorescence* racemose, one–few flowered, erect, terminal; scape lacking sterile bracts; floral bracts foliaceous. *Flowers* resupinate, small, dull-coloured, shortly pedicellate. *Dorsal sepal* free, longer than the lateral sepals. *Lateral sepals* free, smaller than the dorsal sepal. *Petals* free, either larger than the lateral sepals or subsimilar. *Labellum* free, attached by its base to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina membranaceous, not lobed, about as long as wide, flat to concave, margins entire, minutely papillate or crenulate, apex apiculate to acuminate; callus consisting of a large basal, ridge, more or less entire or deeply lobed; nectar absent. *Column* lacking free filament and style, slender, incurved near the apex, sometimes keeled ventrally, sometimes with 1–3 pairs of small marginal teeth; column wings fused to the column, vestigial or absent; column foot absent; anther terminal, two-celled, persistent, basifixed, porrect, rostrate or not; pollinarium present or absent, either all four pollinia attached directly to a viscidium or viscidium absent; pollinia subentire to strongly bilobed, mealy, yellow; rostellum ventral, transverse or two lobed; stigma small, concave, with a prominent, often elongate, entire or bilobed appendage on the lower side. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, thin-walled, erect; pedicels sometimes elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 22.2)

A genus of about 10 species distributed in Japan, Taiwan, northern India, Java, Borneo, Sulawesi, Moluccas, New Guinea, and the Solomon Islands, including Bougainville and Guadalcanal. **(DJ)**

Palynology

Nothing has been published about pollen ultrastructure of *Stigmatodactylus*. **(AP)**

Ecology

Stigmatodactylus is a genus which is poorly understood from both taxonomic and ecological perspectives. Most species occur as individuals or in small groups, apparently reproducing solely from seed. Dispersal of seed following pollination appears to be rapid because some specimens have dehisced capsules together with mature flowers.

Stigmatodactylus have a wide latitudinal range, extending from Japan (about 40° north) to Bougainville and Guadalcanal (about 10° south). They occur mostly at mid-elevations, between about 2000 and 3000 m, although *S. sikokianus* has been reported from as high as 3600 m in Taiwan. They are predominantly terrestrials growing among moss and litter in moist humid forests, particularly rainforest and mist forests. Occasionally plants occur on decaying mossy logs, and they have also been recorded as epiphytes on mossy tree trunks. **(DJ)**

Pollination

Little is known about the pollination of *Stigmatodactylus* species, except that Kores (1991) indicated *S. croftianus* (Kores) Kores and *S. variegatus* (Kores) Kores (as *Acianthus croftianus* Kores and *A. variegatus* Kores) are autogamous. The general similarity of *Stigmatodactylus* and *Acianthus* indicates that outcrossing species of the former may also be pollinated by flies. However, there are no reports of a nectar reward being offered, and the nectar glands found at the base of the labellum in *Acianthus* and *Cyrtostylis* appear to be absent from *Stigmatodactylus*.

Self-pollination in *S. croftianus* and *S. variegatus* occurs when the apical third of the column bends toward the labellum, apparently in response to differential drying. Contraction of the anther expels pollen onto a tooth-like projection at the base of the stigma (Kores 1991). **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Nothing is known about cultivation of these plants. **(HR)**

Taxonomic literature

Kores, P. J. (1991). A revision of the genus *Acianthus* (Orchidaceae) in Papuasia. *Lindleyana*, **6**, 162–73.

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Kores, P. J. (1995). A systematic study of the genus *Acianthus* (Orchidaceae: Diuridae). *Allertonia*, **7**, 87–220.

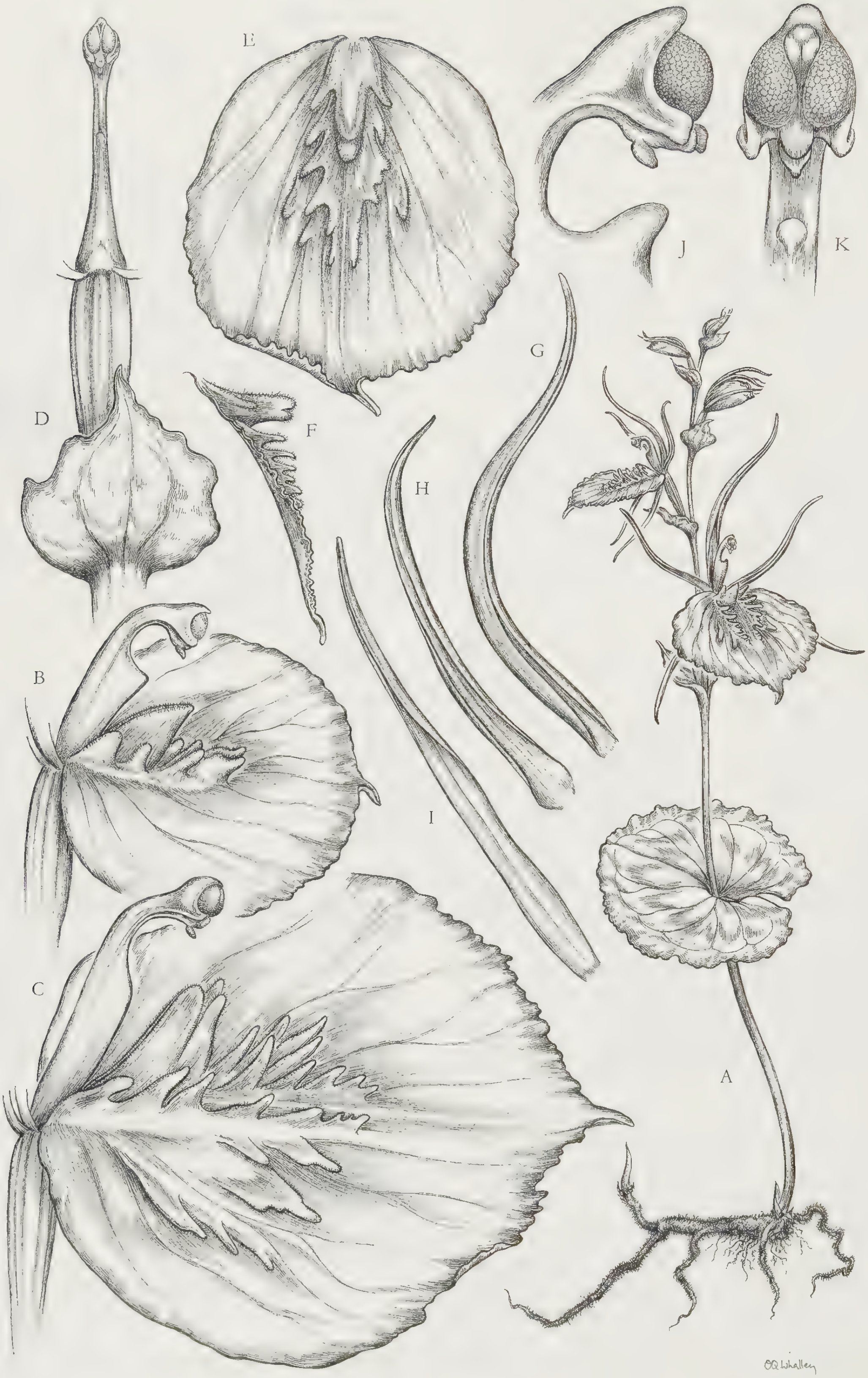

Fig. 22.1. *Stigmatodactylus variegatus* (Kores) Kores. A. Habit, ×1.89; B. Flower from side, perianth removed (Kew Spirit no. 48650), ×8.1; C. Flower from side, perianth removed (Kew Spirit no. 28586), ×8.1; D. Column and bract from front, ×8.1; E. Labellum from above, ×5.4; F. Labellum from side, ×5.4; G. Dorsal sepal, ×5.4; H. Petal, ×5.4; I. Lateral sepal, ×5.4; J. Column apex with anther cap from side, ×27; K. Column apex with anther cap from front, ×27. Drawn by Oliver Q. Whalley from Kew Spirit Collection nos. 48650 and 28586.

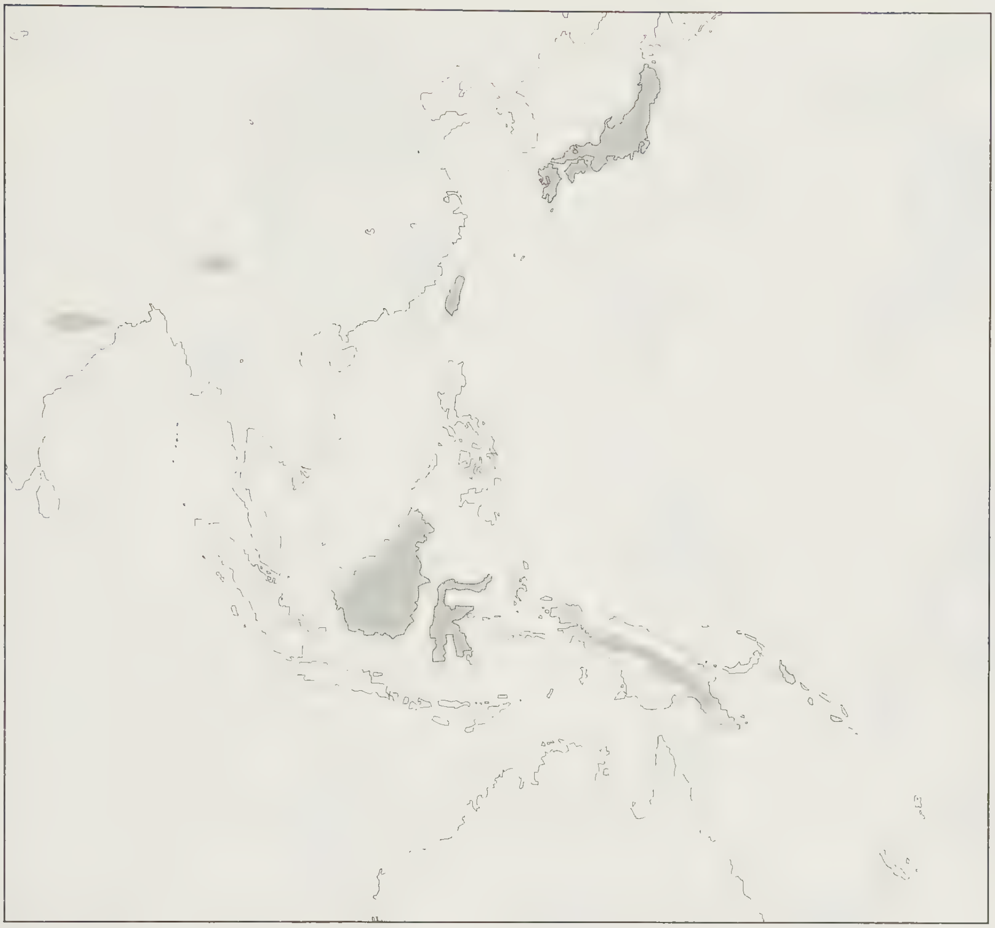

Fig. 22.2. Distribution map of *Stigmatodactylus*.

Schodde, R. (1967). Contributions to Papuasian botany II. A new species of *Acianthus* from Bougainville Island. *Blumea*, **15**, 403–5.

Wood, J. J. and Chan, C. L. (1993). *Pantlingia lamrii*. In *The plants of Mount Kinabalu* (ed. J. J. Wood, R. S. Beaman, and J. H. Beaman), pp. 274–5. Royal Botanic Gardens, Kew.

23. TOWNSONIA

Townsonia Cheesem., *Man. New Zealand Flora*, 691 (1906). Type species: *Townsonia deflexa* Cheesem.

Derivation of name

Commemorating William Townson (1850–1926), English-born pharmaceutical chemist who collected plants in New Zealand. **(DJ)**

Description (Plate 19; Fig. 23.1)

Perennial geophytic *herbs*. *Roots* absent. *Tubers* globose, solitary, small, fleshy; replacement tubers absent; daughter tubers formed at the end of root-like stolons, each tuber shooting soon after its formation and producing a leaf and a new stolon, the stolon remaining extant and linking a series of tubers; subterranean axes lacking papillae. *Stems* short, erect, unbranched, with membranous cataphylls at each node. *Leaf* 1 or 2 from each tuber, basal; lamina extremely membranaceous, flat, convolute in bud, margins crenate; venation anastomosing, the main veins not uniting apically; petiole fleshy, shallowly grooved. *Inflorescence* racemose, 1–3 flowered, erect, terminal; scape lacking sterile bracts; bracts foliaceous, small. *Flowers* resupinate, small, dull-coloured, shortly pedicellate. *Dorsal sepal* free, broader than the lateral sepals. *Lateral sepals* free, narrower than the dorsal sepal. *Petals* free, much smaller than the lateral sepals. *Labellum* free, attached by its base to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina subfleshy, obscurely lobed, folded along the midline, margins entire; callus a narrow thickened central band extending nearly to the labellum apex, lacking any basal glands; nectar apparently absent. *Column* lacking free filament and style, slender, straight, winged throughout; column foot absent; anther terminal, two-celled, persistent, basifixed, porrect, rostrate; pollinarium present, consisting of four pollinia attached directly to a viscidium; pollinia bilobed, mealy, yellow; pollen grains in tetrads; viscidium terminal; rostellum ventral, transverse, almost vestigial; stigma entire, small, concave. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, thin-walled, erect; peduncles elongating in fruit; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

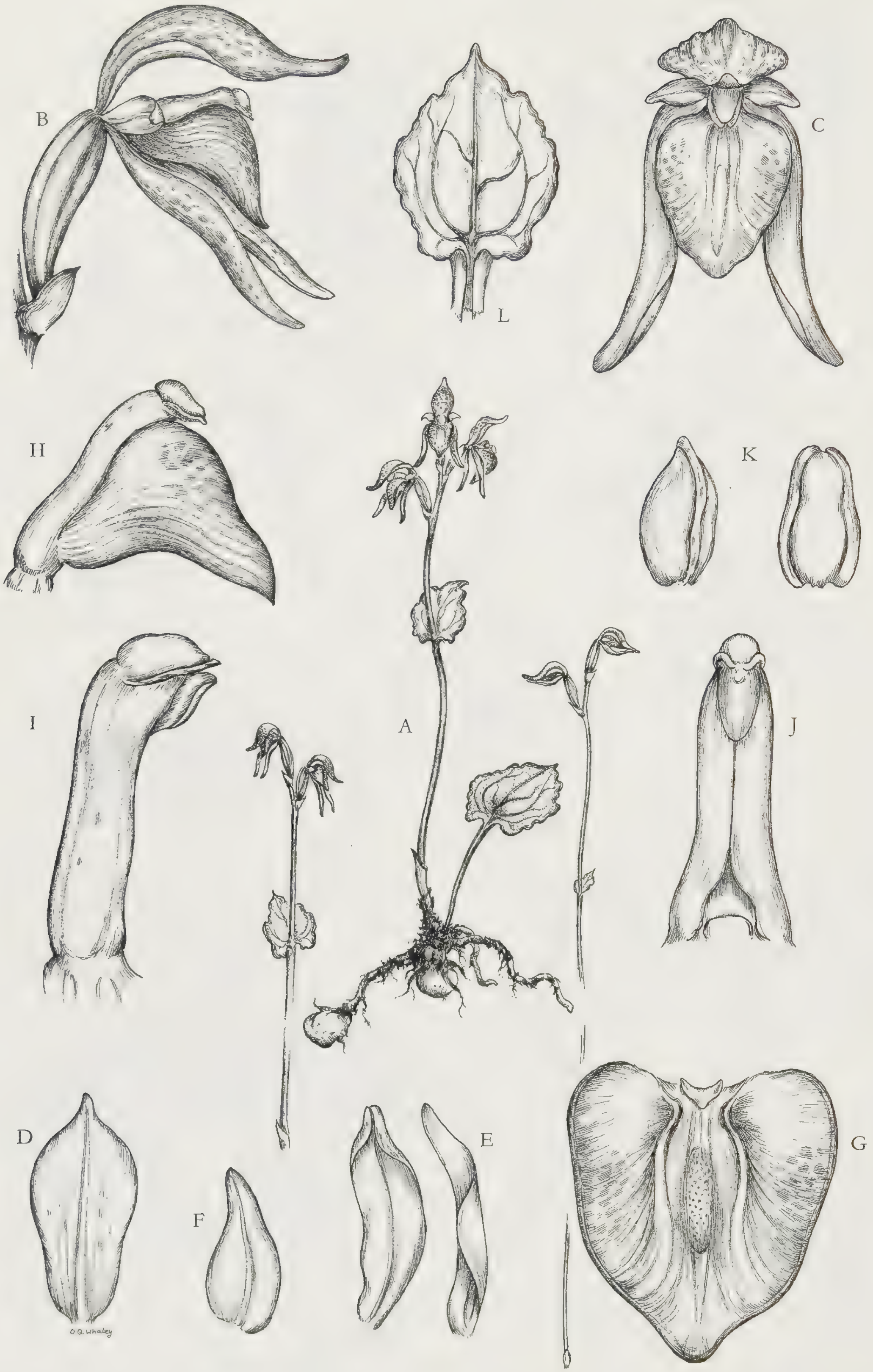

Fig. 23.1. *Townsonia viridis* (Hook.f.) Schltr. A. Habit, ×1; B. Flower from side, ×6; C. Flower from front, ×6; D. Dorsal sepal, ×9; E. Lateral sepal, front and back, ×9; F. Petal, ×9; G. Labellum flattened, from above, ×9; H. Labellum and column from side, ×9; I. Column from side, ×15; J. Column from front, ×15; K. Anther with anther cap, ×21; L. Leaf, ×3. Drawn by Oliver Q. Whalley.

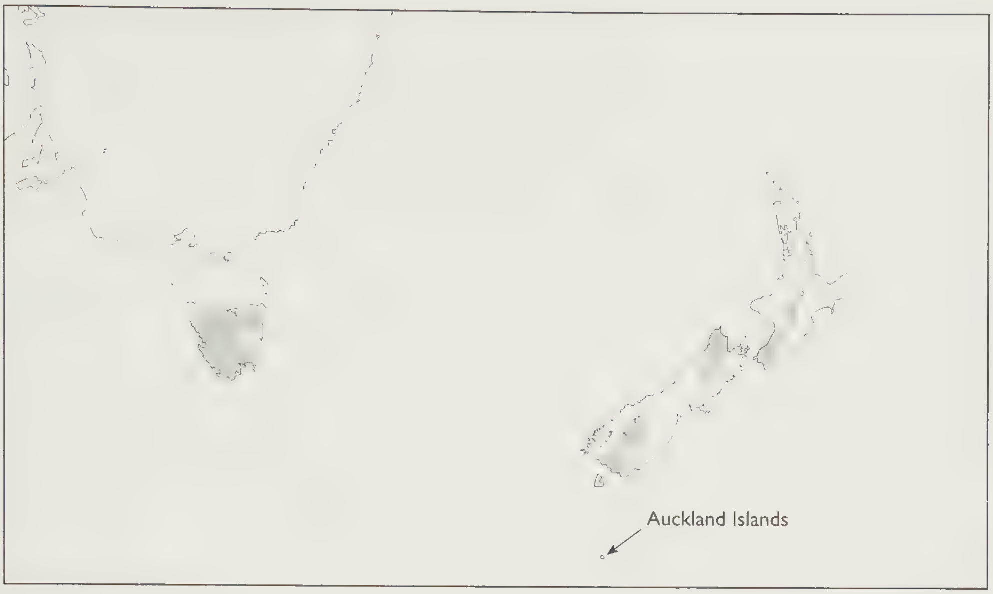

Fig. 23.2. Distribution map of *Townsonia.*

Distribution (Fig. 23.2)

A genus of two species distributed in Australia and New Zealand. *Townsonia viridis* (Hook.f.) Schltr. is endemic to Tasmania, whereas *T. deflexa* occurs in both the main islands of New Zealand and extends south to Stewart Island and Campbell Island. **(DJ)**

Palynology

Nothing has been published about pollen ultrastructure of *Townsonia.* **(AP)**

Ecology

Both species of *Townsonia* grow in dense, permanently moist forests. *Townsonia viridis* occurs almost exclusively in forests dominated by *Nothofagus cunninghamii*, but it is also found in tall eucalypt forest where there is a rainforest understorey. It extends from lowland areas to about 1000 m, between about 41°–43°30' south. The root systems of *Townsonia* plants are not embedded in soil but grow in decaying leaf litter, liverwort carpets, and among mosses on decaying logs and boulders. The fibrous substrate remains damp for much of the year, and humidity is continually high. The plants form small clonal patches in shady situations. Growth occurs mainly in spring and summer (September to March), and the plants are dormant in autumn and winter (April to August). Flowering occurs during late spring and early summer (November to January). After pollination there is some elongation of the peduncle prior to seed release. Swelling of the capsules occurs rapidly, and seeds are shed 2–4 weeks after pollination. **(DJ)**

Pollination

There have been no specific studies of pollination in *Townsonia.* Cady and Rotherham (1970) suggested that the Tasmanian species, *T. viridis*, is self-pollinating and speculated that the position of the anther would allow pollinia to crumble onto the large stigma as flowers age. Molloy (1990) reported that populations of *T. deflexa* in New Zealand are autogamous but gave no information on the mechanism. *Townsonia* lacks the nectar glands found on the labellum of either *Acianthus* or *Cyrtostylis* (Jones 1998*a*) and does not appear to offer food as a reward. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Difficult to maintain in cultivation, even in pots with moss and beech litter. **(DJ)**

Taxonomic literature

Johns, J. and Molloy, B. (1983). *Native orchids of New Zealand.* A. H. & A. W. Reed, Wellington.

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SUBTRIBE CALADENIINAE

Caladeniinae Pfitzer, *Entwurf Anordn. Orch.*, 97 (1887) (as Caladenieae). Type: *Caladenia* R. Br.

Geoblasteae *auct. non* Barb. Rodr.; Burns-Balogh & Funk, *Smiths Contr. Bot.*, **61**, 1–71 (1986).

Description

Hirsute, tuberous, geophytic *herbs*. *Tubers* partly or fully enclosed in a multi-layered fibrous tunic. *Leaf* solitary, convolute, sessile, usually longer than wide, erect to prostrate. *Inflorescence* single-flowered or racemose. *Flowers* resupinate, dull to brightly coloured; tepals subsimilar, variously glandular. *Labellum* hinged to the base of the column, passively motile; lamina three-lobed, the lateral lobes often erect near the column to form a tube, with prominent stalked or sessile calli. *Column* lacking free filament and style; nectar usually absent; column foot absent; pollinarium usually absent; pollinia four or eight. *Fruit* a dehiscent capsule. **(DJ)**

Anatomy

Leaf

SURFACE

Papillae, one per cell, present in *Praecoxanthus* and some species of *Eriochilus*. Hairs multicellular, glandular or nonglandular in *Aporostylis*, *Caladenia*, *Elythranthera*, *Eriochilus*, and *Glossodia*. *Aporostylis* unique in having bi- to triseriate glandular trichomes. Cuticle sculpturing variable, mainly at the generic level, ranging from smooth, crinkled, punctate to striate. Epidermis: cells polygonal or rectangular to elliptical and often axially elongated. Anticlinal walls variable in thickness, but relatively thick with conspicuous pit-fields in all genera except *Adenochilus*. Walls sinuous on one or both surfaces in *Adenochilus*, *Aporostylis*, some species of *Caladenia* and *Cyanicula*, and *Elythranthera*; walls straight in all other taxa. Stomata restricted to abaxial epidermis in *Adenochilus*, some species of *Caladenia*, *Cyanicula*, *Eriochilus*, *Glossodia*, and *Praecoxanthus*. In other genera stomata distributed over both surfaces. Size ranges, mean dimensions, and mean length:width ratios of guard-cell pairs for most taxa are provided in Pridgeon (1993, 1994*b*).

TRANSECTION

Cuticle thin (less than 3 μm), smooth to papillate to striate. Epidermis: cells elliptical, isodiametric to polygonal, the outer wall often differentially thickened, especially at leaf margins. Adaxial cells many times larger than abaxial cells in some species of *Caladenia*, *Cyanicula*, and especially in *Leptoceras*. Stomata superficial, substomatal chambers shallow. Hypodermis present only in *Praecoxanthus*, adaxial, 2–3-layered. Mesophyll heterogeneous or homogeneous according to taxon (Pridgeon 1993, 1994*b*), homogeneous in *Praecoxanthus*. Spongy mesophyll lacunar-stellate in *Elythranthera*, *Eriochilus*, and *Glossodia*. Vascular bundles as for the tribe. Sclerenchyma bundle-caps absent, but some isolated fibres occurring on the abaxial pole of the largest bundles in *Eriochilus multiflorus*. Bundle-sheath two-layered in *Aporostylis*. Ergastic substances: raphides in unmodified chlorenchyma cells and/or mesophyll idioblasts.

Collar/stem

TRANSECTION

Hairs on collar unicellular or multicellular, the multicellular type uniseriate or multiseriate, unbranched, associated with mycorrhiza (Fig. B.2). Hairs on upper portion of stem in *Caladenia*, *Cyanicula*, and *Elythranthera* multicellular, uniseriate, unbranched, nonglandular or glandular depending on species. Cuticle thin, smooth to striate. Epidermis: cells rectangular, elliptical, to polygonal, the outer wall usually thickened. Stomata present or absent depending on taxon. Ground tissue parenchymatous, outer and middle layers of collar usually infected with hyphae and pelotons, the inner layers of stem sclerotic, forming a multilayered sclerenchyma sheath. Cell walls often provided with secondary suberized, banded thickenings. Endodermis of collar: cells elliptical to polygonal with casparian strips. Vascular bundles collateral, often arranged in 1–2 rings with or without a few central bundles, the outer ring frequently abutting sclerenchyma sheath. Xylem tracheids primarily with helical or scalariform thickenings, although annular and pitted occur in some species. Crystals: raphides and/or rod-shaped crystals in cortex and/or ground tissue of most species.

Tuber

TRANSECTION

Hairs absent or present depending on taxon; if present, multiseriate, unbranched, associated with mycorrhiza. Velamen 1–3 layered, cells elliptical to polygonal and often periclinally compressed; walls suberized, of uniform thickness. Simple epidermis in *Caladenia barbarossa* Rchb.f., *Eriochilus multiflorus* Lindl., and *E. scaber* Lindl. Exodermis: cells elliptical to polygonal, walls of uniform thickness or thicker on outer and/or radial walls depending on species. Ground tissue parenchymatous; outer layers often infected with hyphae and pelotons, dissociated with age of tuber. Endodermis: cells elliptical to polygonal. Stele dissected or not depending on taxon; if dissected, 2–10 discrete vascular strands, each 1–13 arch and enclosed by endodermis; if undissected, medullated. Xylem tracheids mainly with scalariform or pitted thickenings. Ergastic substances: starch grains and raphides and/or rod-shaped crystals in ground tissue.

Root

TRANSECTION

Hairs unicellular or multiseriate, associated with mycorrhiza; absent in some genera. Velamen 1–2 (–4) layered, cells elliptical to polygonal; walls of uniform thickness or outer wall and/or radial walls of outermost layer thickened, depending on taxon. Simple epidermis in *Glossodia*, cells anticlinally elliptical to irregular, the outer wall thick and suberized. Exodermis: cells elliptical to polygonal, walls of uniform thickness. Cortex parenchymatous, occasionally infected with hyphae and pelotons, occasionally with starch grains. Endodermis: cells elliptical to polygonal. Stele medullated, 2–12 arch. Xylem tracheids with helical, scalariform, or pitted thickenings. Crystals: raphides or rod-shaped crystals in cortex.

Dropper/Root-like stolon

TRANSECTION

Hairs multiseriate, unbranched, associated with mycorrhiza; absent in *Aporostylis*. Velamen 1–3 layered, cells elliptical to polygonal, walls of uniform thickness or outer walls suberized-thickened. Simple epidermis in species of *Elythranthera*, *Leptoceras*, *Caladenia* (except

C. flava), *Praecoxanthus*; cells isodiametric, dome-shaped, elliptical to polygonal. Exodermis: cells polygonal, walls of uniform thickness. Cortex parenchymatous, outer and/or middle layers often infected with hyphae and pelotons; starch grains infrequent; walls with secondary, banded, suberized thickenings in most species examined. Endodermis: cells elliptical to polygonal. Stele dissected or not depending on species. Older droppers in *Caladenia* and other genera serve as fibrous sheath with secondary wall thickenings, enclosing one or more vascular strands as well as tracheary remnants of older strands. Crystals: raphides or rod-shaped crystals in cortex or pith of medullated steles. **(AP)**

Phytochemistry

Phytochemical data for Caladeniinae are limited to *Elythranthera*, *Caladenia*, and *Glossodia* (see entry under *Elythranthera*). **(NV, RG)**.

Phylogenetics

Caladeniinae was first recognized as distinct within Neottieae because of its unique floral morphology, particularly that of the column. It has variously been treated as part of Diurideae (Dressler 1974, 1981, 1993), Chloraeinae, or Geoblastideae following results of a phylogenetic analysis of the family based mainly on characters and states of floral and pollinia morphology (Burns-Balogh and Funk 1986). The presumed relationships with Chloraeinae or Geoblastideae are entirely artificial; these taxa are closer to Cranichideae than to Diurideae (Clements 1995; Cameron *et al.* 1999; Kores *et al.* 2000).

Recent research using both embryological and molecular techniques (Clements 1995; Kores *et al.* 1997, 2000; Clements *et al.*, in preparation) reveal that Caladeniinae are a distinct group nested among Diurideae. Their previous placements close to Acianthinae and Diuridinae were not unrealistic based on these analyses. **(MAC)**

24. ADENOCHILUS

Adenochilus Hook.f., *Fl. Nov.-Zel.*, **1**, 246 (1853). Type species: *Adenochilus gracilis* Hook.f.

Derivation of name

From the Greek *aden*, gland, and *cheilos*, lip, referring to the labellum calli which are prominent in these orchids. **(DJ)**

Description (Plate 20; Fig. 24.1)

Perennial geophytic *herbs*. *Rhizome* subterranean, fleshy, irregularly cylindrical, long creeping, horizontal, enlarged at each growing point, lacking papillae. *Roots* absent. *Rhizoids* present. *Tubers* absent. *Stem* erect, short, unbranched, with a membranous cataphyll at each node. *Leaf* one per shoot, basal and petiolate or cauline and sessile on the proximal third of a scape; lamina membranaceous, flat, convolute in bud, margins entire, apex apiculate; venation anastomosing, the main veins uniting apically; petiole fleshy, shallowly grooved. *Inflorescence* racemose, 1 (2) flowered, erect, terminal; scape with one or two foliaceous sterile bracts; floral bracts foliaceous,

Artificial key to the genera of Caladeniinae (DJ)

1. • Rootstock a horizontal rhizome with erect stems at intervals; tubers absent .... **24. *Adenochilus***
   • Rootstock non-rhizomatous, 1 shoot per plant, with fleshy tubers 2

2. • Leaf absent from flowering plants, reduced to a thin, scale-like basal bract; leaves on sterile plants ovate, with prominent white veins .... **32. *Praecoxanthus***
   • Leaves similar on both flowering plants and sterile plants, lacking white veins 3

3. • Base of labellum and column forming a tight tube; labellum lamina fleshy, with tufts of eglandular trichomes .... **29. *Eriochilus***
   • Labellum base and column not forming a tight tube; labellum lamina thin, without tufts of eglandular trichomes 4

4. • Leaves usually 2 per shoot; scape lacking a sterile bract .... **25. *Aporostylis***
   • Leaf always 1 per shoot; scape with a sterile bract 5

5. • Leaf glabrous or nearly so; leaves of sterile plants with a small, basal, ligule-like growth; petals clavate, densely covered with sessile red glands; labellum sessile .... **31. *Leptoceras***
   • Leaf densely hairy; leaves of sterile plants without a basal, ligule-like growth; petals never clavate; labellum clawed or sessile 6

6. • Calli restricted to labellum base 7
   • Calli in rows which extend at least to the labellum mid-lobe 8

7. • Flowers glossy; labellum lamina much reduced, thin to membranous, glabrous; column wings hooded above the anther .... **28. *Elythranthera***
   • Flowers dull; labellum lamina well developed, the lateral lobes fleshy, papillate; column wings not extending above the anther .... **30. *Glossodia***

8. • Tubers partly enclosed in a multilayered fibrous tunic; leaf linear to lanceolate; flowers unreactive to weather conditions .... **26. *Caladenia***
   • Tubers wholly enclosed in a multilayered fibrous tunic; leaf ovate; flowers opening fully only in warm weather .... **27. *Cyanicula***

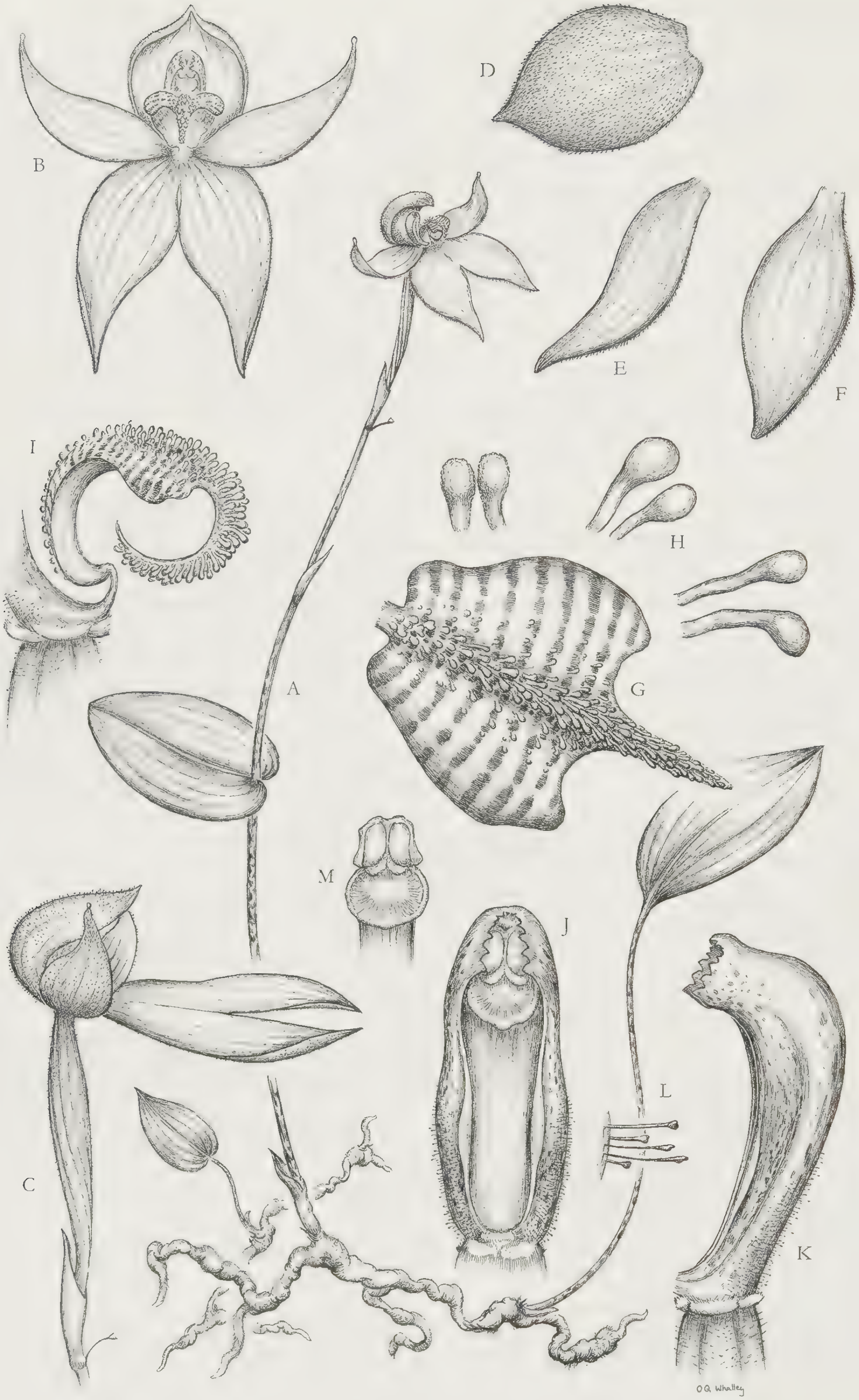

Fig. 24.1. *Adenochilus nortonii* Fitzg. A. Habit, ×1; B. Flower from front, ×3; C. Flower from side, ×3; D. Dorsal sepal, ×3; E. Petal, ×3; F. Lateral sepal, ×3; G. Labellum flattened, from above, ×9; H. Labellum calli, ×21; I. Labellum from side, ×9; J. Column from front, ×9; K. Column from side, ×9; L. Glandular column hairs, ×30; M. Anther and stigma from front, ×9. Drawn by Oliver Q. Whalley.

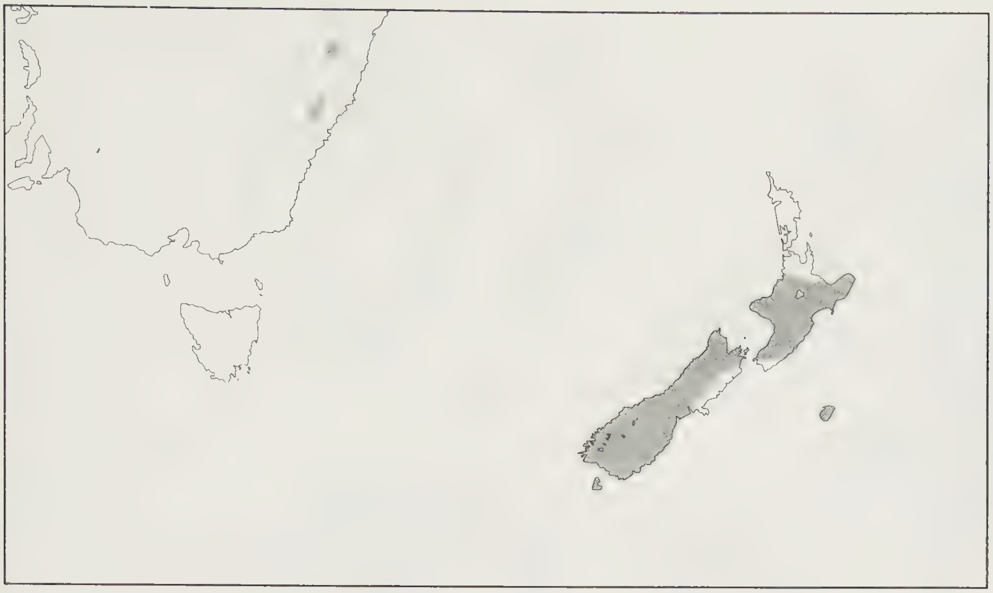

Fig. 24.2. Distribution map of *Adenochilus.*

small. *Flowers* resupinate, dull-coloured, the exterior surface of all parts covered with red glandular hairs, pedicellate. *Dorsal sepal* free, much broader than the lateral sepals, strongly cucullate over the column. *Lateral sepals* free, narrower than the dorsal sepal, porrect. *Petals* free, smaller than the lateral sepals. *Labellum* free, attached by a short claw to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina membranous, distinctly lobed, margins entire; calli clavate, the larger ones in a narrow central band extending from the labellum base to its apex, smaller calli scattered laterally to the main band; nectar absent. *Column* lacking free filament and style, slender, incurved, with red glandular hairs; column wings fused completely, with broadly toothed apices which extend above the anther; column foot absent; anther terminal, two-celled, persistent, basifixed, erect, not rostrate; pollinarium absent; pollinia eight, bilobed, mealy, cream; viscidium absent; rostellum ventral, transverse; stigma entire, small, concave. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, smooth, erect; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 24.2)

A genus of two species distributed in Australia and New Zealand, including Stewart Island and Chatham Island. **(DJ)**

Palynology

Nothing has been published about the pollen ultrastructure of *Adenochilus.* **(AP)**

Ecology

In New Zealand *A. gracilis* Hook.f. is distributed between about 38° south on the west coast of the North Island to about 34° south on Stewart Island. In New South Wales *A. nortonii* Fitzg. is distributed between about 30°30′ south in the New England region to about 34° south in the Blue Mountains. Both species of *Adenochilus* occur in upland to montane habitats. In the northern part of its range the Australian species grows among moss and leaf litter in high rainfall forest dominated by *Nothofagus moorei* (F. Muell.) Krasser, whereas in the Blue Mountains to the west of Sydney it grows among moss in sheltered wet crevices, clefts, and overhangs of sandstone cliffs. *Adenochilus gracilis* grows in moss and liverwort cushions and accumulations of decaying litter in *Nothofagus* forests, mixed forests, and occasionally in scrub on forest margins. Dehiscence takes 8–12 weeks from pollination. **(DJ)**

Pollination

Little is known about the pollination of the two *Adenochilus* species. Jones (1988) stated that the Australian *A. nortonii* is not autogamous or apomictic. The bright white flowers suggest *A. nortonii* is pollinated by nectar- or pollen-seeking insects, such as bees and wasps. The pollination mechanism is likely to parallel those of the similarly structured and coloured flowers of *Caladenia* section *Caladenia.* Pollen mimicry is indicated by the prominent yellow-headed labellum calli. There are no reports of the presence of nectaries in *Adenochilus*, so food deception is the most probable method of pollinator attraction. Self-pollination in *A. gracilis* and many other New Zealand terrestrial orchids may be a response to a lack of pollinators, which in turn is related to the low diversity of insects in New Zealand (Molloy 1990). **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Plants of *Adenochilus* have been maintained in sphagnum moss for short periods of time. **(HR)**

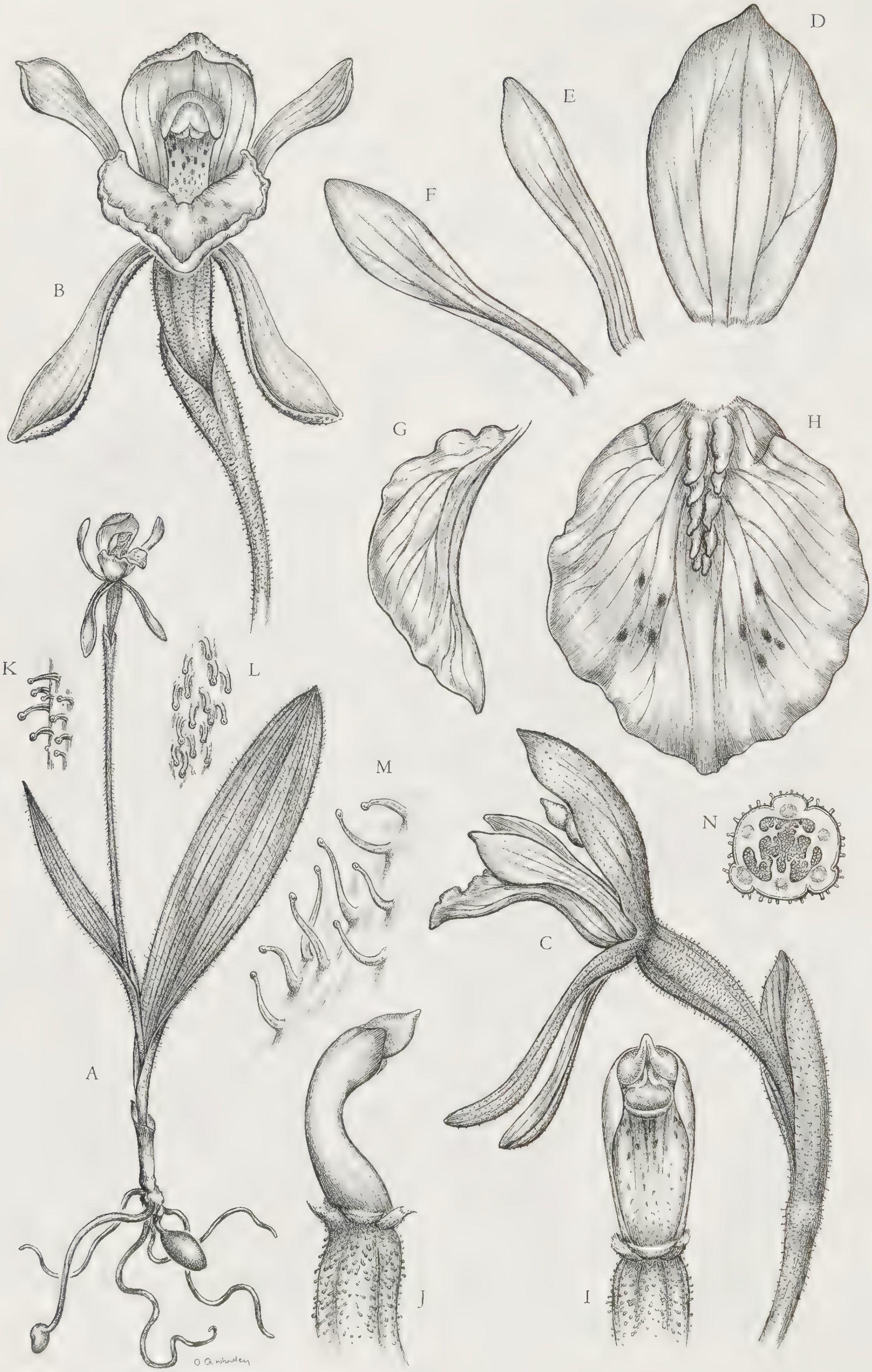

Fig. 25.1. *Aporostylis bifolia* (Hook.f.) Rupp & Hatch. A. Habit, ×0.9; B. Flower from front, ×3.6; C. Flower from side, ×3.6; D. Dorsal sepal, ×5.4; E. Petal, ×5.4; F. Lateral sepal, ×5.4; G. Labellum from side, ×8.1; H. Labellum flattened, from above, ×8.1; I. Column from front, ×5.4; J. Column from side, ×5.4; K. Hairs, ovary, ×18.9; L. Hairs, inflorescence, ×18.9; M. Hairs, leaf, ×18.9; N. Ovary, transverse section, ×8.1. Drawn by Oliver Q. Whalley from Kew Spirit Collection no. 36939.

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25. APOROSTYLIS

Aporostylis Rupp & Hatch, *Proc. Linn. Soc. New South Wales*, **70**, 60–1 (1946). Type species: *Caladenia bifolia* Hook.f. (*Aporostylis bifolia* (Hook.f.) Rupp & Hatch).

Derivation of name

From the Greek, *aporema*, doubt, perplexity, and *stylos*, pillar, column. In general appearance the flowers of this genus appear to contain some elements of both *Chiloglottis* and *Caladenia*, particularly in the column. **(DJ)**

Description (Plate 21; Fig. 25.1)

Perennial geophytic *herbs. Roots* filamentous. *Tubers* obovoid, solitary, small, fleshy; replacement tubers absent; daughter tubers formed at the end of root-like stolons; subterranean axes lacking papillae. *Stem* erect, short, unbranched, with a membranous cataphyll at the apical node. Most above-ground parts with tiny, glandular, multiseriate trichomes. *Leaves* usually two, rarely one, basal, when paired one leaf larger than the other, green with reddish splotches and striations; lamina membranaceous, flat, convolute in bud, hairy, margins entire; venation anastomosing; petiole obvious only on single-leaved plants, fleshy, not grooved. *Inflorescence* racemose, usually 1-(2)-flowered, erect, terminal; scape lacking sterile bracts; trichomes as on leaves; floral bracts foliaceous, small. *Flowers* resupinate, dull-coloured, the exterior of all parts hairy, pedicellate. *Dorsal sepal* free, broader than the lateral sepals, cucullate over the column. *Lateral sepals* free, narrower than the dorsal sepal. *Petals* free, subsimilar to the lateral sepals. *Labellum* free, attached by its base to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina membranaceous, not lobed, margins crenate; callus of two irregular, lobed, thickened central ridges on the proximal third of the lamina; nectar absent. *Column* lacking free filament and style, slender, incurved; column winged throughout; column foot absent; anther terminal, two-celled, persistent, basifixed, porrect, rostrate; pollinia four, bilobed, mealy, naked, cream to pale yellow; rostellum ventral, transverse; stigma entire, small, concave. *Ovary* elongate, ribbed, covered with glandular trichomes. *Capsules* dehiscent, hairy, erect; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 25.2)

A monospecific genus widely distributed in both of the main islands of New Zealand and extending eastward to the Chatham Islands and south to Stewart Island, Codfish Island, Antipodes Island, and the Campbell and Auckland Islands. **(DJ)**

Palynology

Nothing has been published about the pollen ultrastructure of *Aporostylis.* **(AP)**

Ecology

Aporostylis bifolia forms robust extensive clonal colonies in a range of wet, humid habitats along its entire north–south and easterly distribution. Its northern limit is Mt Moehau, 36°30′ south, on the Coromandel Peninsula of the North Island of New Zealand, and its southern limit is about 52° south in the subantarctic Campbell Islands. In the northern parts of its range it is commonly found in montane and upland districts reaching the low alpine zone above tree limit, up to about 1500 m. In the islands and on the western parts of New Zealand's South Island it descends almost to sea level. It thrives in poorly drained peaty soils, in deep moss and bryophyte cushions, especially *Sphagnum* spp., and in a range of mire habitats. It occurs in beech forests, mixed beech/hardwood forests, conifer/hardwood forests, and some more open habitats. In mountainous regions it grows in forest clearings and along forest margins and tussock grassland. In subalpine and alpine zones plants grow in sphagnum bogs under light scrub, herbfield, and in well-drained stony sites. At sea level the species typically occurs in wet sites such as bogs, swamps, and lake margins. It is also known to colonize the deep litter under old forestry plantations of western yellow pine and Corsican pine (Johns and Molloy 1983). Flowering occurs in summer. **(BM, DJ)**

Pollination

No studies into the pollination of *A. bifolia* appear to have been published. Molloy (1990) indicated that it is insect-pollinated, and geitonogamous self-pollination may occur among flowers on the same plant. *Aporostylis bifolia* is not known to produce nectar or an odour and is probably pollinated due to food deception of Hymenoptera. **(CCB)**

Uses

None recorded. **(DJ)**

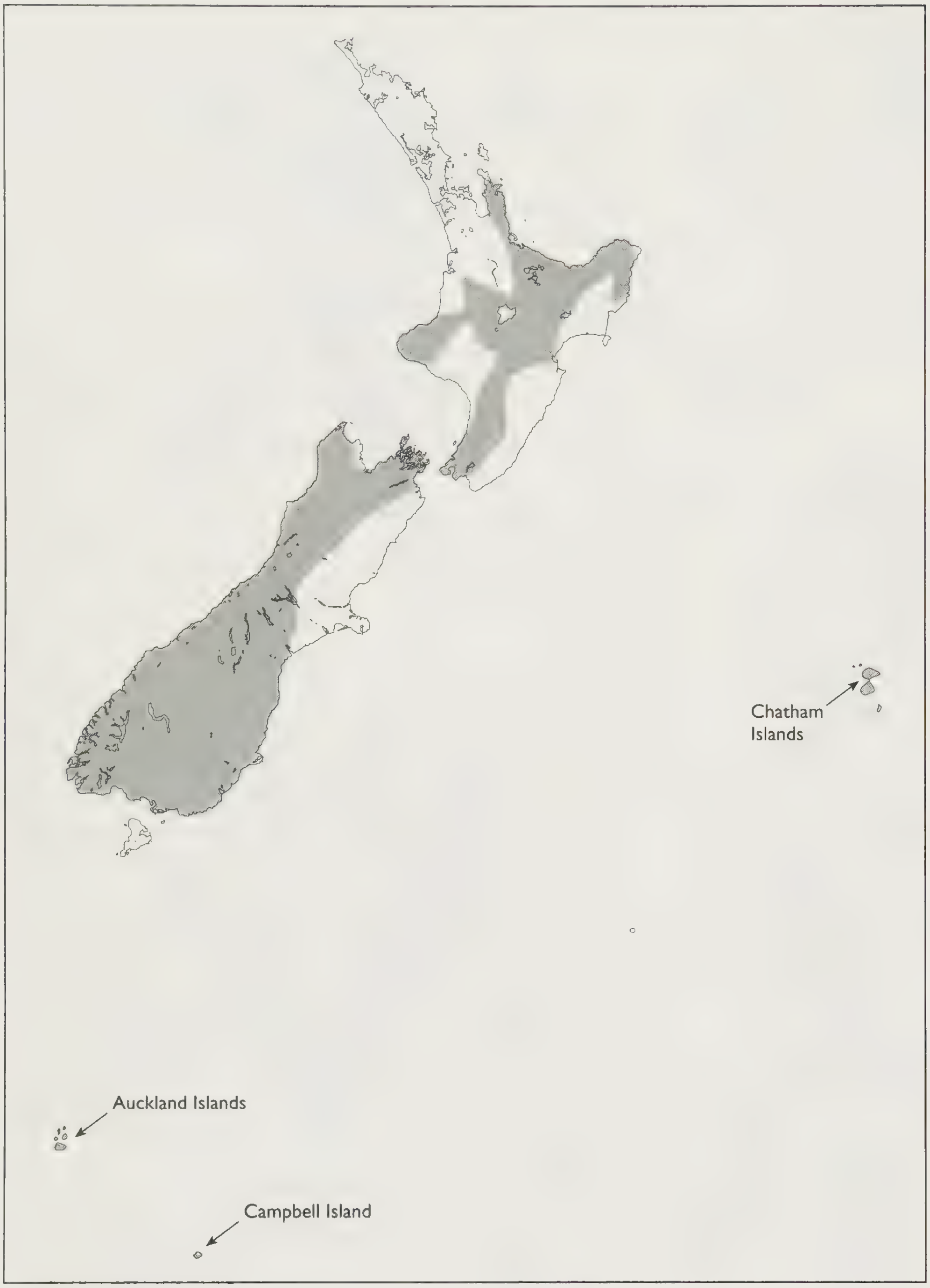

Fig. 25.2. Distribution map of *Aporostylis*.

Cultivation

Plants of *Aporostylis* have been maintained in cultivation for short periods of time only. **(HR)**

Taxonomic literature

Johns, J. and Molloy, B. (1983). *Native orchids of New Zealand.* A. H. & A. W. Reed, Wellington.

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26. CALADENIA

Caladenia R. Br., *Prodr.*, 323 (1810). Type species: *Caladenia carnea* R. Br.

Petalochilus R. S. Rogers, *J. Bot.*, **62**, 65 (1924). Type species: not designated.

Derivation of name

From the Greek *kalos*, beautiful, and *aden*, gland, referring to the prominent, often colourful calli on the labellum. **(DJ)**

Description (Plates 22–25; Fig. 26.1)

Perennial geophytic *herbs*. *Roots* absent or filamentous. *Tubers* globose, paired, fleshy, partly enclosed within a multi-layered persistent fibrous tunic; replacement tubers formed at the end of short droppers; daughter tubers absent in most species or (rarely) formed on the end of slender root-like stolons or on extra droppers. *Stem* erect, short, unbranched, with a membranous cataphyll at the apical node, covered by a multi-layered persistent fibrous tunic to the soil surface. *Leaf* solitary, basal, rarely only partially developed at anthesis, sessile; lamina mostly linear to lanceolate, subcoriaceous, convolute in bud, margins entire; venation anastomosing. *Inflorescence* racemose, 1–few flowered, erect, terminal; scape with one sterile bract; floral bracts foliaceous, sheathing. *Flowers* resupinate, bright to dull-coloured, pedicellate, perianth variously glandular. *Dorsal sepal* free, similar or dissimilar to the lateral sepals, cucullate over the column or spreading. *Lateral sepals* free or rarely fused basally, similar or dissimilar to the dorsal sepal, variously arranged. *Petals* free, similar or subsimilar to the lateral sepals, spreading. *Labellum* free, attached by a short claw to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina obscurely to strongly three-lobed, usually more or less cordate, the margins erect to spreading, entire or weakly to strongly toothed; callus of 2–several longitudinal rows of calli; calli stalked or sessile, clavate, gammate or curved, smooth or papillate, variously coloured, the basal 2–6 calli often different from the rest; nectar usually absent. *Column* lacking free filament and style, slender, incurved, narrowly to broadly winged, the wings translucent and expansive distally; in some species a pair of prominent yellow sessile glands at the base; column foot absent; anther terminal, four-celled, persistent, basifixed, erect, papillate, rostrate; pollinia four, bilobed, flat, mealy, naked, yellow, rarely white; rostellum ventral; stigma entire, circular, concave. *Ovary* elongate, ribbed, covered with glandular trichomes. *Capsules* dehiscent, hairy, erect; pedicels not elongating in fruit. *Seeds* numerous, light- or dark-coloured, winged. **(DJ)**

Distribution (Fig. 26.2)

A genus of about 250 species distributed mainly in Australia but also occurring in New Zealand (including Stewart Island, Chatham Island, and Auckland Island), New Caledonia (including Isle des Pines), and Indonesia (Bali, Celebes, Java, Lombok, and Timor). **(DJ)**

Infrageneric treatment

The following sections have been described within *Caladenia* but are not comprehensive and have limited application until a full revision of the genus can be undertaken. **(DJ)**

Caladenia section **Caladenia** (= **Eucaladenia** Lindl., *Edward's Bot. Reg.*, 1–23*: Swan Riv. Append.*, li (1840)).

Caladenia section **Phlebochilus** Benth., *Flora Austral.*, **6**, 377 (1878). Type species: *Caladenia cairnsiana* F. Muell.

Caladenia section **Calonema** Lindl., *Edward's Bot. Reg.*, 1–23: *Swan Riv. Append.*, lii (1840). Type species: *Caladenia filifera* Lindl.

Palynology

According to Ackerman and Williams (1981), pollen of *Caladenia patersonii* R.Br. var. *longicauda* (Lindl.) R. S. Rogers (= *C. longicauda* Lindl.) is either a globose-spherical monad (*c.* 22 μm) or tetrahedral tetrad (*c.* 36 μm); inaperturate (possibly monoaperturate in monads); tectate-perforate in monads, tectate-perforate tending to semitectate equatorially in tetrads; foveolate and supra-scabrate in monads, foveolate distally but rugulate-reticulate along equator in tetrads. **(AP)**

Ecology

Caladenia has a wide latitudinal distribution, extending from about 7° south in the Lesser Sunda Islands to Auckland Island, which is about 50° south. Species are distributed from near sea level to about 2400 m and occupy diverse habitats. All species of *Caladenia* are terrestrial, most growing as individuals or occurring widely spaced in loose groups or sparse colonies and reproducing solely from seed. A few Australian species also regularly reproduce vegetatively by the production of daughter tubers on the end of root-like stolons to form clonal colonies (for example *C. latifolia* R.Br.) or otherwise by extra droppers to form localized tufts (*C. filamentosa* R. Br., *C. filifera* Lindl.). All species, including those within the tropics, occur in areas with a seasonal climate, and the plants have distinct periods of active growth and dormancy, coinciding with periods of extreme heat or dryness. During these periods the plants survive as small fleshy tubers partly encased in a resistant fibrous sheath, which extends to the soil surface and through which each new shoot develops. The leaves of all species but one are fully expanded prior to flowering, the exception being *Caladenia drummondii* Benth. from Western Australia, which flowers while the leaf is only partially developed. Species of *Caladenia* take 8–12 weeks to mature after pollination.

The greatest concentration and diversity within *Caladenia* occurs in Australia. Within the Australian contingent a number of distinct natural groups can be recognized, the majority of which are endemic to that continent. Some of these, such as *Cyanicula* and *Praecoxanthus*, have recently been proposed as segregate genera (Hopper and Brown, in Hoffman and Brown 1992).

Within Australia *Caladenia* ranges between 15°30′ south and 43° south, with the greatest diversity occurring in the south-eastern and south-western parts of the continent. Most species grow in lowland areas, but one species, *C. alpina*, extends to subalpine zones (up to about 1650 m) where it grows in snowgum woodland, tussock grassland, and herbfield. Common habitats in lowland areas include

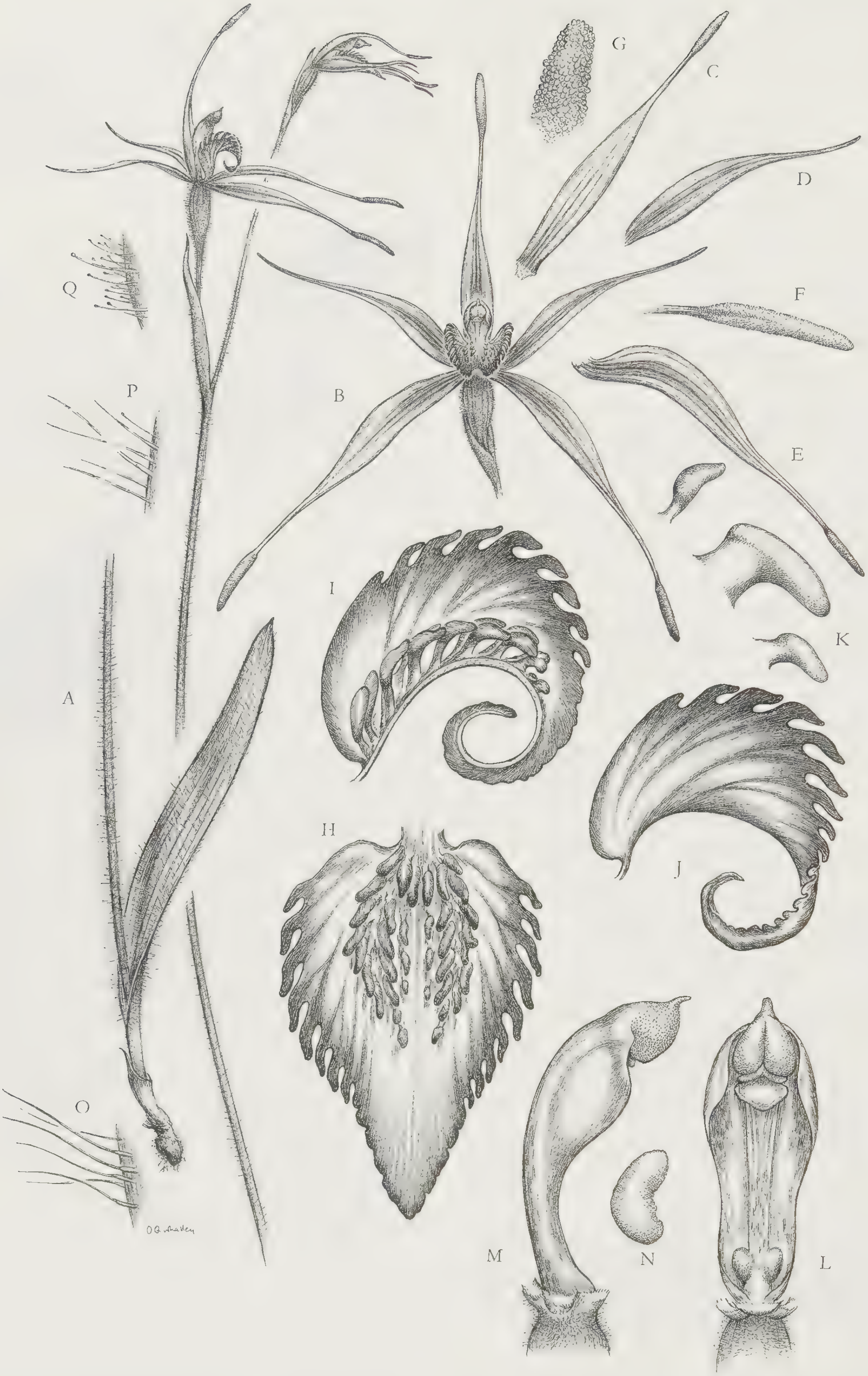

Fig. 26.1. *Caladenia reticulata* Fitzg. A. Habit, ×0.9; B. Flower from front, ×1.35; C. Dorsal sepal, ×1.35; D. Petal, ×1.35; E. Lateral sepal, ×1.35; F. Osmophore, sepal apex, ×5.4; G. Osmophore apex, sepal, ×18.9; H. Labellum from above, ×5.4; I. Labellum, longitudinal section, ×5.4; J. Labellum from side, ×5.4; K. Calli, labellum, ×18.9; L. Column from front, ×5.4; M. Column from side, ×5.4; N. Pollinium, ×8.1; O. Hairs, leaf, ×8.1; P. Hairs, inflorescence, ×8.1; Q. Hairs, ovary, ×10.8. Drawn by Oliver Q. Whalley from Kew Spirit Collection no. 36898.

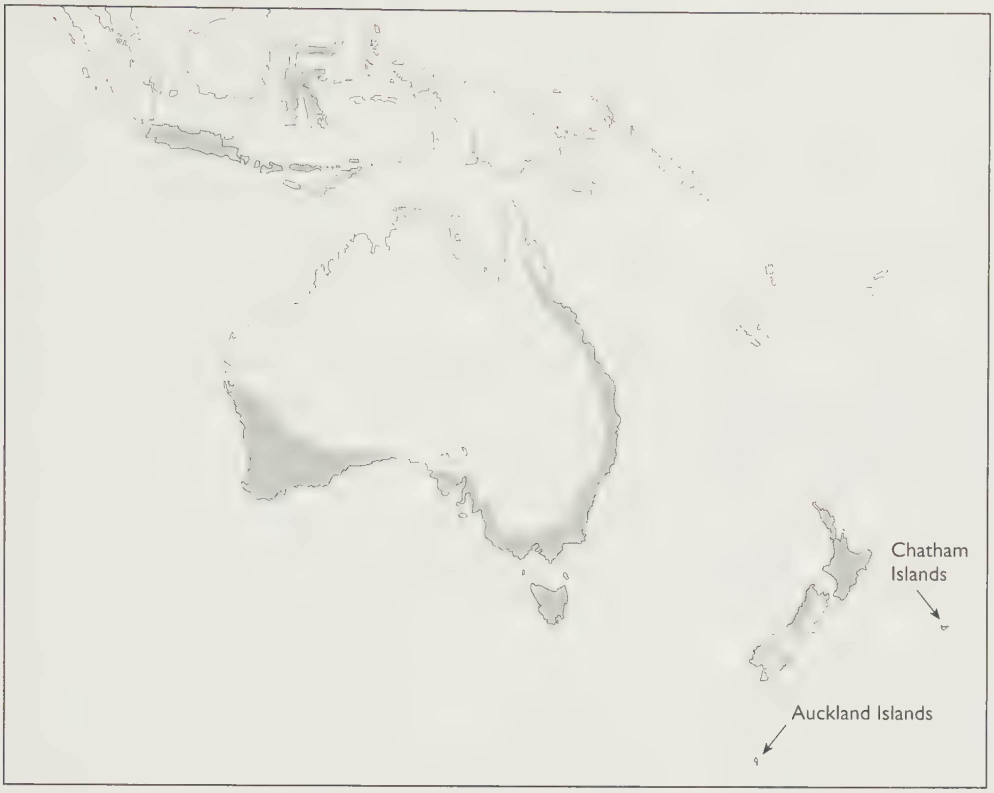

Fig. 26.2. Distribution map of *Caladenia.*

open forest, wet sclerophyll forest, woodland, heathy forests, shrubland, mallee communities (often developed on limestone), coastal scrubs (on both acid and calcareous sands), and heathland. Large granite outcrops are also a significant habitat in Western Australia.

Caladenia species usually occur in well-drained soils, but in Western Australia a few grow in low-lying areas that are moist to wet over winter (for example, *C. radiata* Nicholls and *C. uliginosa* A. S. George). Others occur on sandy rises around the margins of salt lakes (*C. doutchiae* O. H. Sarg.).

The majority of species flower in the spring months between September and November, but a few such as *C. aestiva* D. L. Jones and *C. corynephora* A. S. George flower in early summer. *Caladenia drummondii* is a notable exception, flowering in May and June. Although not fire-dependent, flowering of most Australian species is greatly enhanced by hot fires during the previous summer. Impressive floral displays can result especially where there have been long intervals between burns.

In New Zealand, *Caladenia* occur in a variety of open forest and scrub communities and range from lowland coastal districts to alpine habitats above the treeline. Vegetation types include mixed conifer/broadleaved-hardwood forests, primary and secondary beech forests, primary and secondary scrub communities, and alpine herbfield and tussock grassland. Plants commonly occur in relatively shaded sites among litter and mosses but also may occupy bare ground and frequently colonize track margins and road embankments. A number of species, including *C. atradenia* D. L. Jones and *C. chlorostyla* D. L. Jones, are known to colonize old-growth pine plantations. *Caladenia bartlettii* (Hatch) D. L. Jones has relatively strict requirements, being only found in forests dominated by New Zealand kauri (*Agathis australis* Steud.). *Caladenia lyalli* Hook.f. mostly occurs in upland and subalpine zones, especially in the North Island but can also extend to near sea level in the south. Flowering in New Zealand species occurs between August and January.

The Indonesian species of *Caladenia* all grow in mountainous regions, mostly at elevations between 1200 and 2400 metres, but one species in Bali has been collected between 400 and 550 m. Most of the species from this region grow in grassy patches near forests or on grass-covered ridges and mountain tops, sometimes also in light forest. The soils are usually infertile and fires are frequent in the dry season. Flowering in these species occurs between March and September, depending on the species and elevation.

In New Caledonia *Caladenia* plants occur in grassland and maquis developed on ultrabasic rocky soils. Flowering is mainly between June and October with isolated records in December and January. **(DJ)**

Pollination

The high degree of structural and colour pattern diversity in *Caladenia* is correlated with the evolution of a varied suite of pollinators and pollination mechanisms, and a few species are autogamous or cleistogamous.

Apart from *Caladenia bicalliata* from section *Calonema* and *C. graminifolia*, all self-pollinating species are small-flowered forms in section *Caladenia*, of which some nine species are currently regarded as self-pollinating (Molloy 1990; Jones 1991; Jones *et al.* 1997; Jones 1998*b*). Of these, only *C. cleistantha* D. L. Jones is obligately cleistogamous (Jones 1991). Some plants of *C. bicalliata* R. S. Rogers and *C. vulgaris* D. L. Jones are cleistogamous, but most are autogamous (Jones 1991). In *C. transitoria* D. L. Jones, the lower flowers are autogamous, but the upper ones may be cleistogamous (Jones 1998*b*). In most self-pollinating *Caladenia* species, the flowers open briefly for only a day or two, for example, *C. aurantiaca* (R. S. Rogers) Rupp and *C. mentiens* D. L. Jones in Australia (Jones 1998*b*) and the New Zealand endemics, *C. atradenia*, *C. bartlettii*, *C. chlorostyla*, and *C. nothofageti* D. L. Jones (Jones *et al.* 1997).

Reported insect visitors to outcrossing *Caladenia* flowers include flies, bees, and wasps: all are thought to be attracted by deceptive mechanisms involving the false offer of food or sexual rewards (Stoutamire 1983; Adams and Lawson 1993). However, many of the reported observations are anecdotal; there have been few systematic scientific studies and in many cases the pollinator status of the visitors or the mechanism of attraction is not clear (Adams and Lawson 1993).

It is generally agreed that flowers of *Caladenia* offer no reward to pollinators (Rogers 1931; Bates 1982; Stoutamire 1983; Dafni and Bernhardt 1990; Adams and Lawson 1993). There is no evidence of nectar secretion; flowers are usually borne singly on the stem in contrast to reward-offering terrestrial genera such as *Prasophyllum*, *Microtis*, and *Spiranthes*, and insect activity around flowers is low.

Food deception appears to be the dominant pollination syndrome in the small-flowered *Caladenia* species of section *Caladenia*, but scientific evidence is lacking. The bright pink, white, and yellow hues are typical of plant species advertising the presence of food rewards to nectar- and pollen-gathering insects (Faegri and van der Pijl 1979). The upturned labellum side lobes and prominent column wings of *Caladenia* species form a curved 'floral tube' below the column. Longitudinal rows of yellow, orange, or reddish calli line the central labellum lamina within and sometimes outside the tube. It is likely these are pollen mimics.

The first observations of pollination were by Fitzgerald (1875–1893), who reported self-pollination of *C. dimorpha* Fitzg. by a house-fly (probably *Musca domestica*) and *C. catenata* (J. J. Sm.) Druce (reported as *C. alba* R.Br.) by an unidentified fly. Rogers (1931) regarded these reports as atypical on the basis that the events described by Fitzgerald 'lacked the purposive character which usually marks the act of pollination in orchids under natural conditions'.

Erickson (1965), Ulherr (1967), and Bates (1982) have so far provided the only observations of outcrossing pollination in section *Caladenia*. Erickson (1965) observed the activities of native bees, *Paracolletes nicholsonii*, on *C. flava*. *Caladenia flava* R. Br. and similar species such as *C. latifolia* R.Br., *C. nana* Endl., and *C. reptans* Lindl. have a curved row of tall labellum calli at the throat of the tube formed by the bases of the labellum and column. Erickson (1965) observed small male and larger female *P. nicholsonii* attempting to enter the tube. The calli formed a 'palisade', effectively barring entry to the small males, but the larger females easily surmounted the barrier and forced their way to the base; pollination was not observed, however. Erickson (1965) concluded the palisade excludes 'small and ineffectual' insects from entering. This may be important because it is not uncommon for small insects to stick to the stigma of *Caladenia* species and, lacking the strength to pull free, die, thereby blocking the flower for visitors of the correct size (C. Bower, unpublished). It is also common for excessively large insects to block flowers and die. After forcing their way into the throat, the thorax or wing bases of large insects may become wedged against the anther preventing their escape (Erickson 1965).

In most section *Caladenia* species 'palisade' calli are absent. Visiting insects of the correct size must force their way into the narrow floral tube by pushing the labellum downward with their legs. This action thrusts the thorax into the sticky stigma between the column wings. Pollinia on the insect's thorax break up and are smeared across the stigmatic surface. Not all pollen is usually removed so that one vector may pollinate several flowers.

Immediately distal to and abutting the stigma is a rudimentary crescent-shaped rostellum that secretes a viscid glue onto the thorax of the retreating insect. Most accounts of pollination in the Caladeniinae attribute the sticky coating of the pollinator's thorax to stigmatic secretions (e.g. Rogers 1931; Erickson 1965; Cady and Rotherham 1970; Stoutamire 1974*a*; Peakall and Beattie 1996). However, only the secretion of the rostellum is readily removed and coats the dorsal surface of the retreating insect's thorax immediately before it contacts the anther.

Ulherr (1967) observed the removal of pollinia from the anther of a flower of *C. alba* (now *C. catenata*) by a syrphid fly backing out of the flower. The pollinia of Caladeniinae are covered by two triangular anther flaps attached to the outer edges of the anther by their antero-lateral margins, so they are held closed as the insect enters the flower. However, when it backs out, its thorax catches the free basal margins lifting the flaps and exposing the pollinia (Erickson 1965), which adhere to the sticky rostellar secretion and are pulled free.

Bates (1982) suggested the pollination of the bright pink flowers of *C. congesta* R.Br. by the colletid bee, '*Hylapus* sp.' (probably *Hylaeus* sp.; Adams and Lawson 1993), represented an example of sexual deception or pseudocopulation. The labellum calli of *C. congesta* have broad smooth black heads forming a solid mass resembling the body of the pollinating bee (Bates 1982). Visiting bees 'alighted directly onto the calli of the labellum mid-lobe, and would shake it vigorously for 3–5 seconds before crawling into the space between the labellum and column' and 'each bee would place its legs on either side of the dark calli' (Bates 1982). The shaking behaviour is almost certainly an example of buzz pollination (Buchman 1983). The mass of dark labellum calli probably mimics the poricidal anthers of common species of Hemerocallidaceae and Laxmanniaceae which are shaken by bees to liberate pollen through pores and slits onto their bodies. This, coupled with the bright pink perianth coloration, indicates that pollination of *C. congesta* is an example of food deception, not pseudocopulation (Adams and Lawson 1993).

Among section *Calonema*, only the large white-flowered species in the *C. patersonii* R.Br. and *C. filamentosa* complexes appear to be food-deceptive (Stoutamire 1975, 1983). Species in the *C. patersonii* complex attract a variety of nectar- and pollen-feeding insects, mainly Hymenoptera (Tiphiidae, Colletidae, Apidae, and Halictidae) and Diptera (Calliphoridae, Tachinidae, and Syrphidae) according to Stoutamire (1983). Erickson (1965) found the native bee, *Euryglossa rejecta*, with pollinia of the white-flowered *C. filamentosa* R.Br. var. *tentaculata* R. S. Rogers on its thorax. The flowers of *C. patersonii* emit strong musky odours from concentrations of trichomes at the tepal apices and sweet odours from the labellum (Stoutamire 1983). The labellum is rigidly attached to the base of the column, in contrast to many of the sexually deceptive section *Calonema* species, and functions in the same way as in the food-deceptive species of section *Caladenia*. According to Stoutamire (1983) the labellum 'is moved downward by insects forcing their way under the column'. This is also true of *C. filamentosa*, despite the assertion by Erickson (1965) that it has a mobile labellum (C. Bower, unpublished).

Dafni and Bernhardt (1990) suggested *C. patersonii* represents an intermediate state between food deception and sexual deception on the basis that the labellum calli may be reddish and thynnine wasps are attracted to the flowers. However, Adams and Lawson (1993) point out that Stoutamire (1983) did not identify which of the floral visitors were successful pollinators, if any, and it is premature to assign *C. patersonii* to the sexual deception syndrome. Stoutamire (1975, 1983) considered that thynnine visitors to *C. patersonii* were seeking food, not mates. An additional complication is that many new taxa (Carr 1991; Jones 1991, 1998*b*; Hoffman and Brown 1992) have been identified in the *C. patersonii* complex since Stoutamire (1975, 1983) made his observations. It is not known which of these attracted the various visitors he collected.

However, observations by Bates (1984*c*) and Bickerton (1997) provide some evidence for a mixed food deception/sexual deception pollination syndrome in the rare *C. rigida* R. S. Rogers. Native bees, *Exoneura* spp., enter flowers, move to the base of the labellum, and remove or deposit pollinia as described above. Bates (1984*c*) suggested that *C. rigida* may be a food mimic of *Burchardia umbellata* R.Br. (Colchicaceae), which also has white flowers with reddish markings and is visited by the same bees. Bickerton (1997) observed a single unidentified male thynnine wasp moving in 'figures of eight' for ten minutes on the outside of a bag placed over a *C. rigida* flower. The behaviour indicated that the male was searching for a female and trying to enter the bag. Similar behaviour by thynnine males has been observed by the author on the outside of nets and cages placed over sexually deceptive *Chiloglottis* species (C. Bower, unpublished). This observation indicates that *C. rigida* may emit mimics of thynnine sex pheromones from its prominent sepal glands. More observations are needed to clarify the nature of *C. rigida* pollination.

Pollination by sexual deceit in *Caladenia* appears to be confined to sections *Calonema* and *Phlebochilus* (Stoutamire 1974*a*, 1975, 1983; Bower 1992; Peakall and Beattie 1996) and is the main pollination syndrome of those sections, encompassing over 130 species. All sexually deceptive *Caladenia* species appear to be pollinated by species of thynnine wasps in specific relationships such that each orchid is adapted for pollination only by a single wasp species (Stoutamire 1983; Bower 1992, 1993, 1996*b*, 1997). This specificity is thought to be mediated primarily through the emission by each orchid species of specific odours that mimic the sex pheromones emitted by receptive female thynnines to attract males for mating (Stoutamire 1975, 1983; Peakall and Beattie, 1996).

The unique life cycle of thynnine wasps appears to have lent itself to exploitation by deceptive orchids. Females are wingless, an adaptation for burrowing in the soil in search of beetle larvae to parasitize. Periodically females emerge from the soil and may climb the stems of low grasses and herbs from where they attract males by emitting volatile sex pheromones into the air from mandibular or abdominal glands (Plate 26).

Males generally respond very rapidly to calling females; it is not uncommon to see a dozen or more males converging on a female. The first male to find the female quickly grasps her behind the head with his forelegs and flies rapidly upward to avoid competing males. Copulation may take place at first contact or later when the pair settles on vegetation. When not responding to females, males spend much of their time patrolling low over the ground to intercept any new pheromone trail.

A coupled male takes the female to a nectar or honeydew source, all the while remaining in copula. Modes of feeding vary among thynnine genera. Some species allow the female to feed directly from the food source, in others the male imbibes the nectar and regurgitates it to the female. In some species, for example *Tachynomia* spp., the male carries a bubble of nectar held in a special set of curved hairs in a cavity below the head. This is given to the female before copulation takes place (Given 1954). After feeding the male returns the female to the ground, often simply releasing her in flight about 20 cm above the soil surface. The female quickly burrows to resume her search for larvae to parasitize.

The flowers of sexually deceptive *Caladenia* species possess a number of distinctive adaptations for thynnine pollination. They are generally coloured in dull shades of green, cream, brown, or off-white with patches of dark maroon on the labellum, particularly the apex (Stoutamire 1974*a*, 1983). The labellum calli are usually dark red or maroon with stout columns and thick heads and are densely clustered to mimic the body of a female thynnine wasp resting on the labellum, for example, *C. macrostylis* Fitzg. and the *C. dilatata* R.Br. complex. Labellum mobility due to a flexible joint with the base of the column is another common adaptation.

However, some sexually deceptive species have flowers that bear little resemblance to a female thynnine and are not dissimilar to those of *C. patersonii*, for example the *C. huegelii* Rchb.f. complex. *Caladenia huegelii* has calli that, although red, are short and widely spaced, collectively showing no similarity to an insect body. However, the bright red background coloration of the labellum lamina may provide a visual mimic of the female. Stoutamire (1983) found that *C. huegelii* attracts males of a black thynnine wasp of the genus *Zaspilothynnus*, which approach flowers in a zigzag flight as they follow the pseudopheromone odour trail upwind. Wasps crawl up the centre of the relatively immobile labellum between the upturned fringed margins and move below the column. It is likely the male is seeking the head region of the female both to verify her mandibular pheromone signals and to grasp her behind the head with his forelegs (Bower and Logan, unpublished) for a nuptial flight. The thorax of the male contacts the stigma and deposits pollinia or becomes stuck to the viscid surface. The wasp must reverse out to extricate itself and may remove pollinia after passing the rostellum. Stoutamire (1983) found the source of the pseudopheromone to be the dense trichomes on the tips of the tepals. No odour appeared to be emitted by the labellum or column. It seems that odour attracts males from a distance and that visual cues such as labellum colour provide the close range stimuli.

By contrast to *C. huegelii*, which appears to have minimal physical adaptations for sexual deception, other *Caladenia* species have developed a variety of specializations. Members of the *C. dilatata* complex are characterized by a mobile labellum, a dark maroon labellum apex, and thick reddish black labellum calli arranged in dense clusters along the labellum mid-line. The mobile labellum rotates about its attachment to the base of the column through a shifting balance mechanism analogous to a see-saw (Erickson 1965; Stoutamire 1983). An attracted wasp usually alights on the maroon labellum apex, postulated to be a visual female mimic (Stoutamire 1983), the weight pulling the labellum downward. The wasp then crawls toward the labellum base, the shifting weight first returning it to its normal position, then causing it to fall suddenly against the column. As the wasp backs out of the trap, its thorax contacts the stigma (where pollinia may be deposited) and then the rostellum, which smears it with glue, enabling removal of pollinia from the anther. Once it has cleared the anther, the shifting weight distribution allows the labellum to fall open again.

Caladenia multiclavia Rchb.f. represents an extreme variation on the shifting balance mechanism (Stoutamire 1983). In this species the base of the column is held horizontally, and the labellum lamina is held parallel to it on a long vertical claw. A dense cluster of dimorphic calli on the lamina represents the pseudofemale; a broad band of red-tipped calli mimics the female body with darker calli at the basal end of the lamina representing the head. Male *Tachynomia* sp. (Thynninae) are induced to fly in above the decoy by having the pseudopheromone glands higher than the mobile labellum on the upturned tips of all tepals. Alighting males attempt to grasp the decoy and are tipped upside down into a cradle formed by highly developed column wings and lobes of the petal bases that embrace the column. The tipping process is likely to be assisted by the male's attempts to fly off with the labellum decoy, which would cause the labellum to rotate about its hinge plunging the wasp against the column. Males can only escape by reversing between the column wings.

The unusual labella of *Caladenia barbarossa* and its relatives have long been recognized as insect mimics (Sargent 1907), although it was not until 1974 that the true nature of the mimicry was proven (Stoutamire 1974*a*). Sargent (1907) guessed the pollinator of *C. barbarossa* might be a predatory insect attracted by the sight of potential prey. However, the black wasps he observed on flowers showed 'gentle' behaviour rather than the expected aggressive interaction. From the position adopted by the wasps on the labellum, Sargent (1907) concluded they were gaining nectar from the large black central callus, the pseudoinsect head, projecting toward the column from the base of the labellum lamina.

The wasps grasped the narrow base of this callus with their legs, which aligned their heads with the bulbous pseudohead and their bodies around the reddish hairy lamina of the labellum. This position is typically adopted by male thynnine wasps when picking up females for nuptial flight, except that Sargent's (1907) illustration shows all three pairs of legs around the neck region instead of just the forelegs (Bower and Logan, unpublished). It is not likely that all legs would be used because this would prevent the male from landing on vegetation to feed her.

Coleman (1930*a*) suspected that *C. barbarossa* was pollinated by pseudocopulation. She observed that visiting wasps did not attempt to feed on the basal calli but gripped the labellum tightly and embedded the abdomen in the calli. Pseudocopulation was confirmed by Stoutamire (1974*a*) when he observed the black males of *Thynnoides bidens* making copulatory movements with their abdomens on the labellum. Males approached the flowers by typical zigzag upwind flight within the odour trail. They grasped the mobile labellum and, in attempting to fly away with it, caused it to rotate rapidly about its flexible attachment to the column foot, throwing the wasp head downward against the column. As in all other thynnine-pollinated flowers pollination occurs when the wasp backs out along the labellum past the stigma, where incoming pollen is deposited, and then the rostellum coats the thorax with glue, securing pollinia from the adjacent anther. Once the wasp clears the anther, the labellum falls back to its original position.

Of the 130 or more species of *Caladenia* likely to be pollinated by sexual deception, thynnine wasps have so far been actively attracted to 35 by baiting with flowers in the field (Bates 1989*b*; 1996; G. Brown and C. Bower, unpublished). Only a small proportion have been verified as pollinators (Adams and Lawson 1993). No insects other than thynnine males have been observed on these species.

Stoutamire (1983) concluded that within a local area each sexually deceptive species of *Caladenia* had only one pollinator. However, he noted that different wasp species may respond to orchids taken outside their normal geographical ranges. He also found that different races in the *C. dilatata* complex attracted different thynnine wasp species. These were postulated to be examples of geographic pollinator replacement. However, recent taxonomic studies have concluded that *C. dilatata s.l.* comprises a complex of distinct species. It is likely therefore that the 'races' tested by Stoutamire (1983) now represent distinct species, each with a single specific pollinator.

The latter interpretation is supported by experimental studies showing that *C. phaeoclavia* D. L. Jones and *C. tentaculata* Schltdl.

consistently attract different thynnine species, *Lophocheilus anilitatus* and *Thynnoides pugionatus*, respectively, in field choice tests (Bower 1992, 1993). Bower (1996*b*, 1997) showed that closely related cryptic or sibling species of *Caladenia* can be distinguished by their pollinator specificity in field choice tests. For example, tests show that two co-occurring cryptic species with different thynnine pollinators exist within *C. concinna* (Rupp) D. L. Jones & M. A. Clem. and allopatrically within *C. tentaculata* in New South Wales. The significance of pollinator specificity is further demonstrated by the fact that *C. montana* G. W. Carr and *C. fitzgeraldii* Rupp, which were synonymized by Clements (1993), have different species of *Phymatothynnus* as pollinators (Bower 1996*b*). Conversely, these methods have shown that some widespread variable species may have been oversplit taxonomically; for example, *C. phaeoclavia* and *C. parva* G. W. Carr are both pollinated by the thynnine, *Lophocheilus anilitatus*, and could be interpreted as the same biological species (Bower 1996*b*). In the case of sexual deception, pollinator specificity may provide a valuable adjunct to systematic study.

Despite the high degree of pollinator specificity in sexually deceptive species, there are many reports of natural hybrids (Nicholls 1969; Heberle 1982; Hoffman and Brown 1984). However, given the extensive recent taxonomic revision of *Caladenia* (e.g. Carr 1991; Jones 1991; Hoffman and Brown 1992), it is not clear how many of the purported hybrids have now been given species status. Even with this uncertainty, hybrids may occur among members of the food-mimicking *C. patersonii* complex and sexually deceptive groups such as the *C. dilatata* complex (Stoutamire 1983; Hoffman and Brown 1992). Stoutamire (1975, 1983) proposed that these hybrids arose from interspecific transport of pollen by thynnine wasps responding at different times to food and sexual stimuli.

Some key characteristics of pollination by sexual deception in *Caladenia* were revealed in a study of *C. tentaculata* by Peakall and Beattie (1996). The primary pollinator, *Thynnoides pugionatus* (Thynninae), was rarely seen on flowers *in situ* in the field but was readily attracted to bait flowers placed away from field colonies. Responses to bait flowers initially were numerous but declined rapidly to zero within 10–15 minutes of their placement. Experiments showed that wasps avoid flowers after an unsuccessful visit thereby accounting for the low levels of activity around flowers in nature.

The avoidance reaction was shown to result in much longer distance dispersal of pollen between flowers than is seen for food-rewarding species but was limited by the relatively small female search ranges of males, about 40–60 m (Peakall and Beattie 1996). The avoidance reaction minimizes inbreeding, which in *C. tentaculata* may result in lower seed production and slower development of seedlings. These selective advantages may account for the evolution of the sexual deception pollination syndrome but do not explain the high degree of subsequent diversification in the genus *Caladenia*.

In general the frequency of attempted mating on the flower by visiting wasps is low, 7.5% in the case of *C. tentaculata* (Peakall and Beattie 1996), which indicates that the short-range mimicry of females is not convincing to most wasps. Peakall and Beattie (1996) suggested that only inexperienced males or those with a low stimulus threshold due to lack of previous mating success will mate with the decoy. An alternative explanation may be that males learn to avoid flowers at close range after many fruitless encounters with them.

Strong competition among males for the limited supply of above-ground females may be a key driver in the system (Peakall and Beattie 1996), lowering male discrimination. However, excessively vigorous interactions with the flower may result in self-pollinations when males persist in attempting to mate after having removed the pollinia. Between 3% and 10% of pollinations in *C. tentaculata* may be selfings (Peakall and Beattie 1996). **(CCB)**

Uses

Caladenia species are only grown as ornamentals by specialist growers (see below). **(DJ)**

Cultivation

Caladenia is one of the most popular and showy genera of Diurideae, many species of which will grow well in the hands of an experienced grower. However, several species are difficult to maintain.

Mix: basic but with extra drainage material added, for example an extra one fifth portion of coarse sand. Light: 25%–35% shade. Watering: keep moist from mid-autumn until mid to late spring. Flowering: mainly from late winter to late spring. Propagation: some species are colony-formers. Others grow into clumps. Most are solitary species and do not respond well to tuber removal. These are propagated from seed sprinkled around a parent plant or by laboratory flasking.

Caladenia tubers rot easily. Great care must be taken to ensure that they are potted in a well-drained mix and that they are not overwatered. Watering should be commenced later than that for many other genera and continued until mid- or late spring, ceasing as the leaves start to yellow with the onset of dormancy. **(HR)**

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27. CYANICULA

Cyanicula Hopper & A. P. Brown. Type species: *Caladenia gemmata* Lindl. (*Cyanicula gemmata* (Lindl.) Hopper & A.P. Brown)

Caladenia R. Br. sect. *Pentisea* Lindl., *Edward's Bot. Reg.*, 1–23, *Swan Riv. Append.*, liii (1840). Type species: not designated.

Derivation of name

From the Greek *cyano-*, blue, and the diminutive suffix *-icula*, small, alluding to the small blue flowers of these orchids. **(DJ)**

Description (Plates 27, 28; Fig. 27.1)

Perennial geophytic *herbs*. *Roots* absent. *Tubers* globose, paired, fleshy, enclosed fully within a multi-layered persistent fibrous tunic; replacement tubers formed within the tunic on the end of short droppers; daughter tubers absent. *Stem* erect, short, unbranched, with a membranous cataphyll at the apical node, covered by a multi-layered persistent fibrous tunic to the soil surface. *Leaf* solitary, basal, sessile; lamina mostly ovate to linear, subcoriaceous, convolute in bud, margins entire; venation anastomosing. *Inflorescence* racemose, 1–few flowered, erect, terminal; scape with one sterile bract; floral bracts foliaceous, sheathing. *Flowers* resupinate, mostly blue, rarely yellow or white, pedicellate; perianth variously glandular, in the majority of species expanding in response to light and temperature. *Dorsal sepal* free, similar or subsimilar to the lateral sepals, erect to spreading. *Lateral sepals* free, similar or dissimilar to the dorsal sepal. *Petals* free, similar or subsimilar to the lateral sepals. *Labellum* free, attached by a short claw to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina unlobed to strongly three lobed, the margins erect to spreading, entire or weakly to strongly toothed, the underside sometimes with clusters of papillae; callus of 2–several longitudinal rows of calli; calli stalked or sessile, clavate, gammate or curved, smooth or papillate, variously coloured, the basal 2–6 calli often different from the rest; nectar absent. *Column* lacking free filament and style, slender, incurved, narrowly to broadly winged; column foot absent; anther terminal, four-celled, persistent, basifixed, erect, papillate, rostrate; pollinia four, bilobed, flat, mealy, naked, yellow; rostellum ventral; stigma entire, circular, concave. *Ovary* elongate, ribbed, covered with glandular trichomes. *Capsules* dehiscent, hairy, erect; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 27.2)

A genus of nine species distributed mainly in southern Australia, most occurring in Western Australia. **(DJ)**

Palynology

Nothing has been published about pollen ultrastructure of *Cyanicula*. **(AP)**

Ecology

Species of *Cyanicula* are found in a range of sclerophyll forests and shrublands with some species occupying specific niches, such as stabilized coastal dunes and shallow soils over granite sheets. All species are terrestrials growing in loose groups and reproducing solely from seed. They occupy areas that have a strong seasonal climate, and the plants grow actively in autumn and winter and flower in spring. Flowering is greatly promoted by summer fires. Dehiscence occurs 8–12 weeks after pollination. **(DJ)**

Pollination

Cyanicula species are unique in all having blue flowers except for two taxa in the *C. gemmata* complex that have yellow or white flowers. Apart from the labellum, *Cyanicula* species have similar, lance-

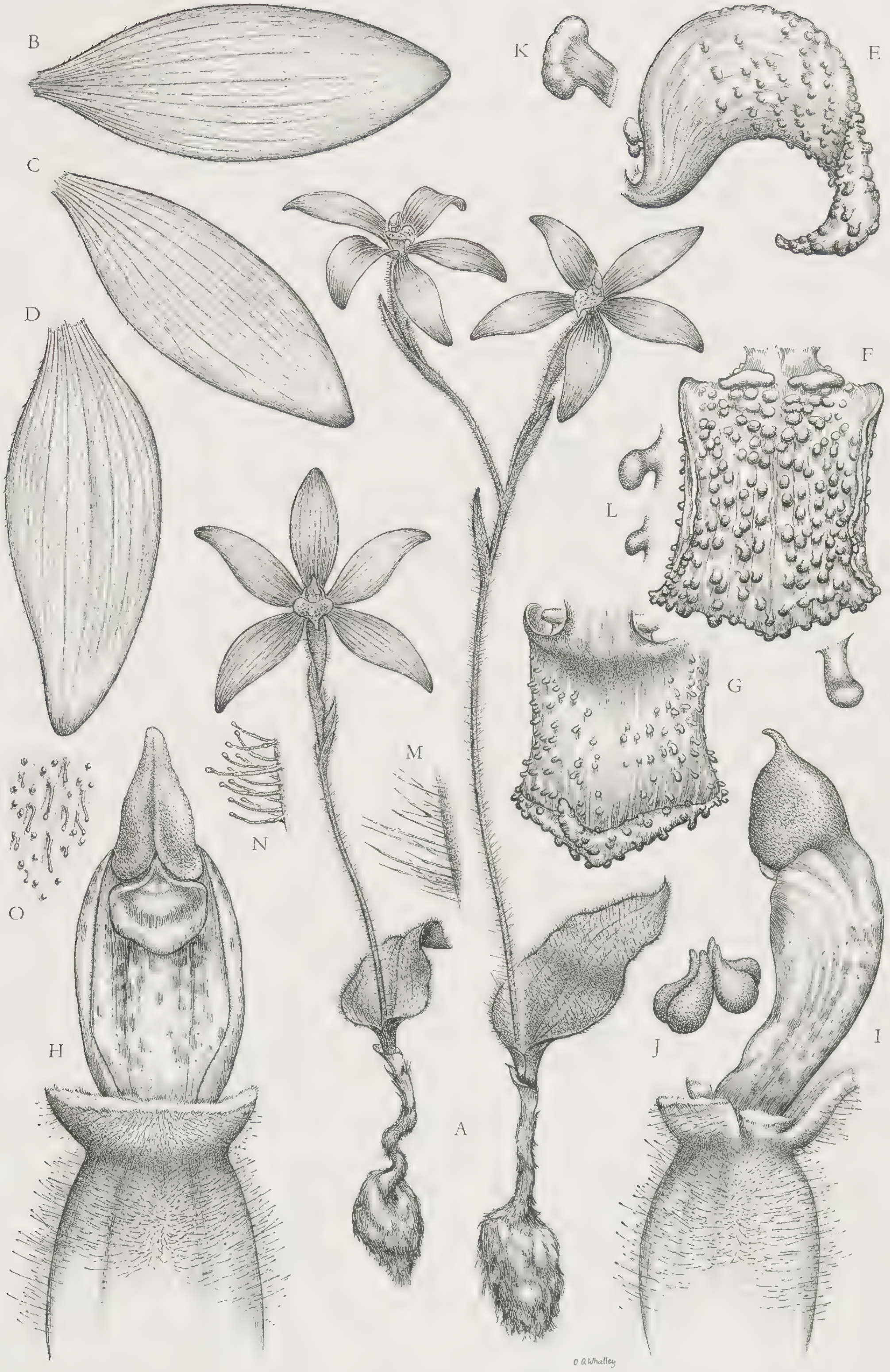

Fig. 27.1. *Cyanicula gemmata* (Lindl.) Hopper & A. P. Brown. A. Habit, ×0.9; B. Dorsal sepal, ×2.7; C. Petal, ×2.7; D. Lateral sepal, ×2.7; E. Labellum from side, ×8.1; F. Labellum from above, ×8.1; G. Labellum from below, ×8.1; H. Column from front, ×8.1; I. Column from side, ×8.1; J. Pollinia, ×8.1; K. Basal callus of labellum, ×10.8; L. Distal calli, ×18.9; M. Hairs, inflorescence, ×8.1; N. Glandular hairs, ovary, ×13.5; O. Glands and glandular hairs, outer surface of perianth, ×13.5. Drawn by Oliver Q. Whalley from Kew Spirit Collection no. 47088 (as *Caladenia gemmata* Lindl.).

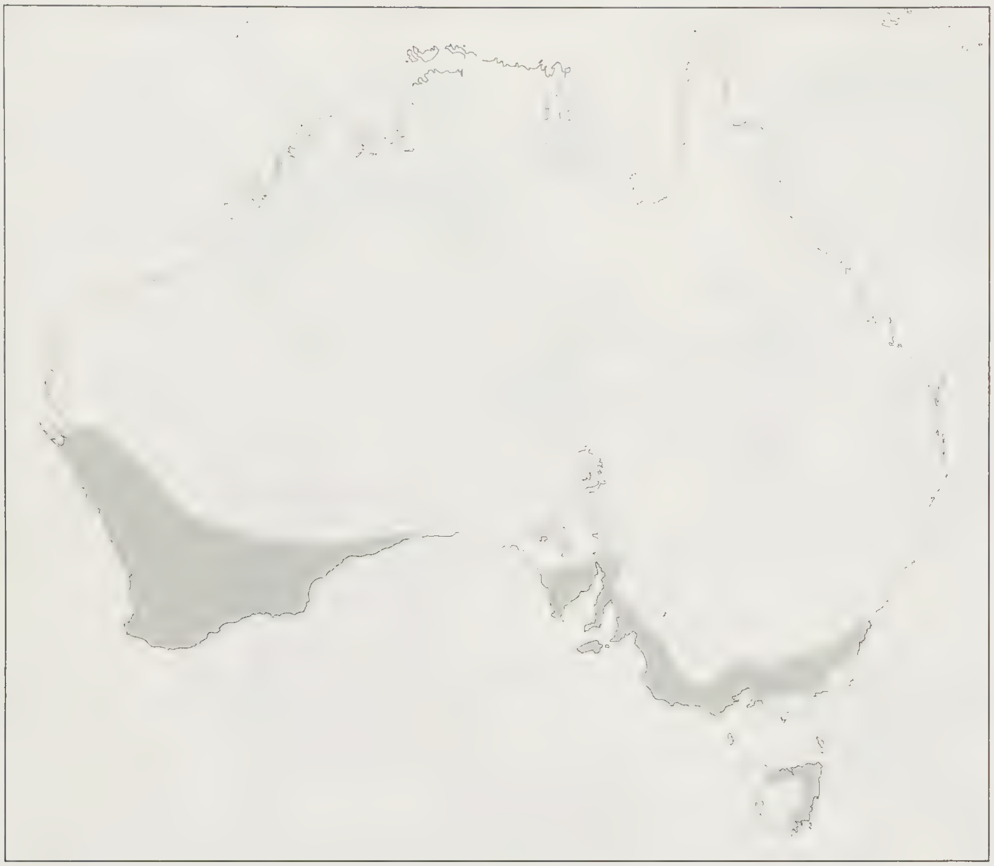

Fig. 27.2. Distribution map of *Cyanicula.*

shaped, radially arranged tepals characteristic of many food-advertising plants (Faegri and van der Pijl 1979). Nectar appears to be absent (Rogers 1931; Peakall 1987) and, like all orchids, pollen is not offered as a food reward. Some species, particularly members of the *C. gemmata* complex, have strong, sweet odours likely to function in pollinator attraction.

Rogers (1931) reported and corroborated observations by Goldsack on pollination of *C. deformis* (R.Br.) Hopper & A. P. Brown by the native bee, *Halictus subinclinans.* Both found the insect would move into the tube formed by the horizontal labellum, its upturned side lobes, and the overhanging column. Longitudinal rows of dense calli on the central lamina of the labellum become taller toward the base, thereby narrowing the opening. As a bee moves farther into the tube it is forced to push the labellum outward, which in turn presses its thorax between the broad column wings into the sticky, bowl-shaped stigma, resulting in pollination if the bee has pollinia on its thorax. The pollinia, as in all Caladeniinae, are mealy and break up when smeared over the stigma; they may be only partially removed from the bee's thorax, allowing it to pollinate more than one flower. Rogers (1931) suggested bees were attracted to tall glandular calli covered in stellate hairs at the base of the labellum. At the deepest point of penetration only the tip of the bee's abdomen was visible at the orifice of the tube.

Rogers (1931) observed that bees removed pollinia from the anther only as they retreated from the tube. He noted that a 'very viscid' 'rudimentary rostellum' is found at the base of the anther. This narrow inconspicuous crescent-shaped structure closely abuts the upper margin of the stigma and is often overlooked. Curiously, Rogers (1931) stated that the pollinator's thorax was coated in stigmatic secretion rather than that from the rostellum. As indicated above for *Caladenia*, the stigmatic surface is not easily removed and appears to be adapted solely to collect pollen; it is the rostellum that supplies the glue for pollinia removal. Anther function in *Cyanicula* species is the same as for *Caladenia.*

Cyanicula gemmata is pollinated by nectar scarab beetles of the genus *Neophyllotocus* (Melolonthinae: Sericini; Peakall 1987). Species of *Sericini* tend to mass on flowering plants where they feed and mate. Peakall (1987) observed two species, *N. legnotus* and *N. rostratus*, effectively pollinating many *C. gemmata* flowers in the Darling Range near Perth, Western Australia (Plate 28). After a mass emergence thought to be synchronized by rain, *N. legnotus* was observed in abundance on freshly opened flowers of *C. gemmata* and other species, with numbers declining gradually on subsequent days. The beetles were most active between about 10 am and 1 pm after which they rested passively on flowers of a variety of species.

Pollination occurred when beetles bearing pollinia on the pronotum (top of the thorax) forced their way down the tube formed by the labellum and column. Beetles would remain in the tube for some minutes occasionally sweeping the base of the column with their mouthparts in an apparent search for nectar (Peakall 1987). In this position the pollinia were pressed against the stigma, effecting pollination. As the beetles retreated a new load of pollinia was acquired. Beetles were observed to accumulate multiple pollinia and to pollinate several flowers. Pollinia were being carried by an estimated 35% of the beetle population. Some 55% of flowers in the study population were pollinated (Peakall 1987).

Neophyllotocus legnotus appear to have quite short adult lives, and during this time are attracted to a variety of rewarding and non-rewarding flowers (Peakall 1987). Feeding appears to be largely opportunistic, and beetles show little capacity to avoid non-rewarding species. Flowers may serve as much as resting sites and meeting places for mates as feeding sites. Peakall (1987) observed *N. legnotus* feeding on nectar on a *Drosera* flower and on disrupted pollinia, which had been partially removed from two *C. gemmata* flowers. Although the beetles were attracted to flowers of *Cyanicula sericea* (Lindl.) Hopper & A. P. Brown, they were too large to enter the small floral tube. *Caladenia gemmata* flowers most prolifically after fires in the previous summer. This may reduce competition with mass-flowering shrub species for the attentions of swarming *Neophyllotocus* species.

Observations of beetle flight patterns indicated the potential for pollinia to be transported relatively long distances, up to 23 m in a single flight, indicating that *C. gemmata* is likely to be a highly outcrossing species. This was verified by genetic analysis of five polymorphic enzyme loci using cellulose acetate electrophoresis. Genetic distances among populations were low. The same alleles tended to be dominant in all populations, and there was a high degree of genetic individuality among plants. The results were consistent with a random mating, predominantly outbreeding species.

Peakall (1987) found there was no genetic differentiation among three populations of the blue-coloured *C. gemmata* and one of its white-coloured near relatives, *C. ixioides* (Lindl.) Hopper & A. P. Brown subsp. *candida* Hopper & A. P. Brown. Pollination of the yellow-flowered *C. ixioides* subsp. *ixioides* by *N. xanthipennis* was photographed by Stoutamire (quoted in Peakall 1987). Isolated flowers of both subspecies of *C. ixioides* successfully set seed among populations of *C. gemmata*, indicating cross-pollination among the colour types. The sharing of *Neophyllotocus* pollinators, sympatric distributions, and lack of genetic differentiation led Peakall (1987) to conclude that the evidence for taxonomic differentiation of *C. gemmata* and *C. ixioides* (Hoffman and Brown 1992) is weak. Rather, they appear to be colour forms of a single species. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Treat as for *Caladenia*. These are difficult to maintain long in cultivation. **(HR)**

Taxonomic literature

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28. ELYTHRANTHERA

Elythranthera (Endl.) A. S. George, *West Austral. Nat.*, **9**, 6 (1963). Type species: *Glossodia brunonis* Endl. (*Elythranthera brunonis* (Endl.) A. S. George).

Glossodia R.Br. sect. *Elythranthera* Endl., *Nov. Stirp. Dec.*, **2**, 16 (1839).

Derivation of name

From the Greek *elytron*, sheath, and Latin *anthera*, anther, referring to the apical parts of the column wings that extend over the anther. **(DJ)**

Description (Plate 29; Fig. 28.1)

Perennial geophytic *herbs*. *Roots* absent. *Tubers* globose, paired, fleshy, enclosed within a multi-layered persistent fibrous tunic; replacement tubers formed within the tunic on the end of short droppers; daughter tubers absent. *Stem* erect, short, unbranched, with a membranous cataphyll at the apical node, covered by a multi-layered persistent fibrous tunic to the soil surface. *Leaf* solitary, basal, sessile; lamina mostly lanceolate, subcoriaceous, convolute in bud, margins entire; venation anastomosing. *Inflorescence* racemose, 1–3 flowered, erect, terminal; scape with one sterile bract; floral bracts foliaceous, sheathing. *Flowers* resupinate, brightly coloured, glossy, pedicellate. Sepals and petals subsimilar, glandular externally. *Dorsal sepal* free, spreading. *Lateral sepals* free, porrect. *Petals* free. *Labellum* free, attached by its base to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina unlobed, ligulate to subulate, folded or sharply recurved distally, the margins entire; callus reduced to one or two basal calli; calli antheriform, ornamented, on a flattened claw; nectar absent. *Column* lacking free filament and style, straight, broadly winged, the wings translucent and expansive distally, extending apically as a hood over the anther; column foot absent; anther terminal, four-celled, persistent, basifixed, erect, papillate, rostrate; pollinia four, lobed, flat, mealy, naked, pale yellow; rostellum ventral; stigma entire, quadrate, concave. *Ovary* elongate, ribbed, covered with glandular trichomes. *Capsules* dehiscent, hairy, erect; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 28.2)

A genus of two species endemic in south-western Western Australia. **(DJ)**

Palynology

Nothing has been published about pollen ultrastructure of *Elythranthera*. **(AP)**

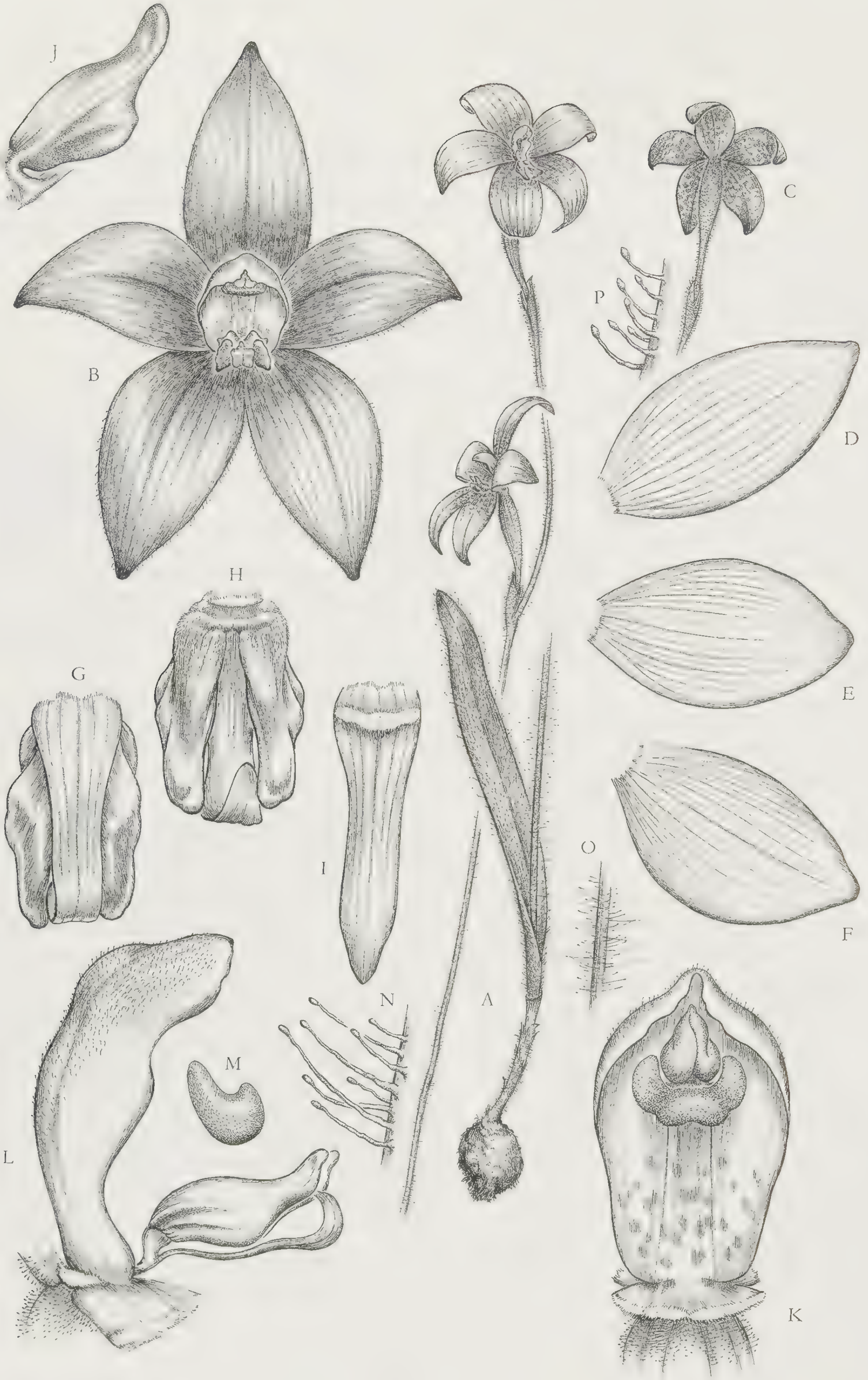


Fig. 28.1. *Elythranthera brunonis* (Endl.) A. S. George. A. Habit, ×0.9; B. Flower from front, ×2.7; C. Flower from behind, ×0.9; D. Dorsal sepal, ×2.7; E. Petal, ×2.7; F. Lateral sepal, ×2.7; G. Labellum from below with basal calli, ×8.1; H. Labellum from above with basal calli, ×8.1; I. Labellum, flattened, showing position of attachment of basal calli, ×8.1; J. Basal callus of labellum from side, ×5.4; K. Column from front, ×5.4; L. Column from side with labellum and calli, ×8.1; M. Pollinium (after David L. Jones), ×8.1; N. Enlargement of glandular hairs on inflorescence, ×18.9; O. Enlargement of hairs and glandular hairs, ×18.9; P. Enlargement of glandular hairs, ovary, ×18.9. Drawn by Oliver Q. Whalley from Kew Spirit Collection no. 47035.

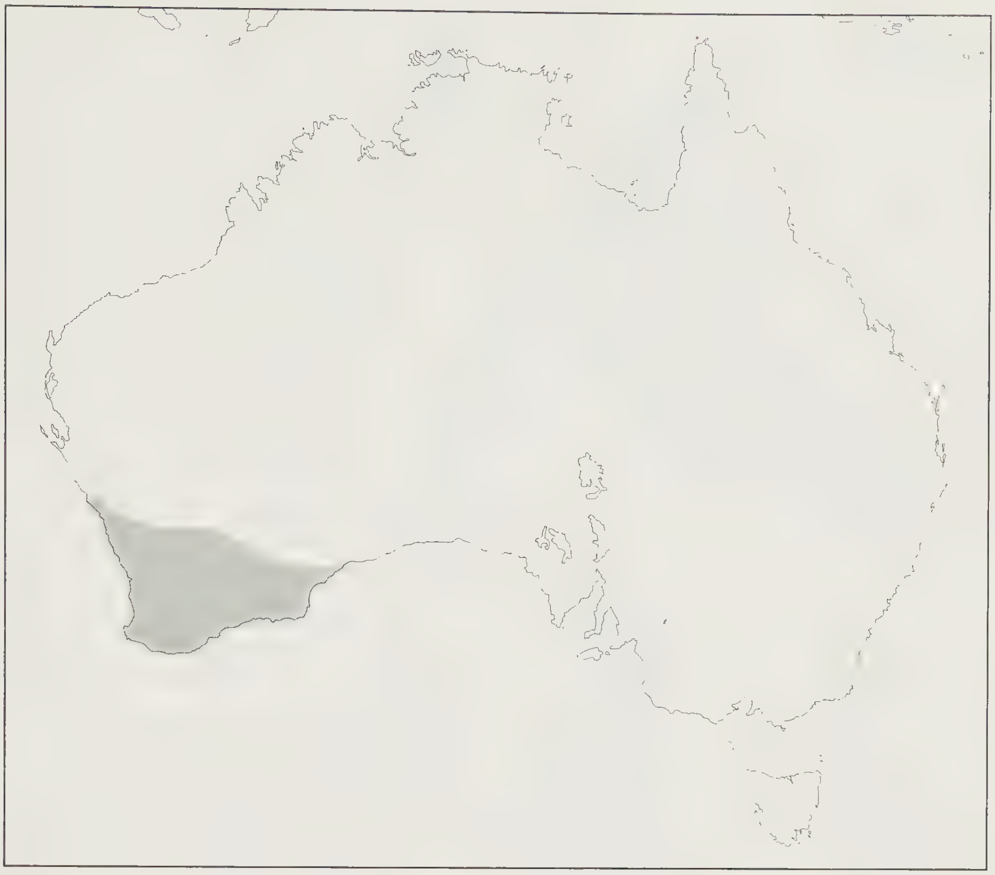
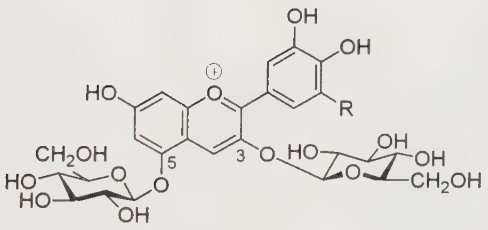


Fig. 28.2. Distribution map of *Elythranthera.*



1 R = H
2 R = OH

Fig. 28.3. Anthocyanins of *Elythranthera.* (**1**) Cyanidin 3,5-diglucoside (cyanin), (**2**) delphinidin 3,5-diglucoside (delphin).

Phytochemistry

Two anthocyanins, cyanidin 3,5-diglucoside and dephinidin 3,5-diglucoside, have been identified in the flowers of both *E. brunonis* and *E. emarginata* (George *et al.* 1973; Strauss *et al.* 1974). In terms of dry tissue weight, *E. brunonis* and *E. emarginata* contain 1.2% and 2.9% anthocyanins, respectively. The flowers of both species contain approximately twice as much cyanidin 3,5-diglucoside as dephinidin 3,5-diglucoside (Fig. 28.3).

The origin of blue flower colours (those of *E. brunonis* are purple-blue) is structurally complex and usually requires a coloured anthocyanin, a flavonoid copigment, and one or more metal ions in a macromolecular assembly. The occurrence of potential flavonoid copigments in flowers of *Elythranthera* has not been investigated to date. George *et al.* (1973) used anthocyanin content in *Elythranthera* and the genera *Caladenia*, *Glossodia*, and *Thelymitra* to discuss chemotaxonomic and ecological relationships among these taxa. The anthocyanins in the last three genera were not identified definitively. **(NV, RG)**

Ecology

Both *E. brunonis* and *E. emarginata* (Lindl.) A. S. George occur in a range of habitats, including woodland dominated by *Eucalyptus wandoo* Blakely and *Banksia* spp., shrubby forest dominated by *Eucalyptus marginata* Sm., shrubland, and heath. *Elythranthera emarginata* tends to favour wetter sites and extends into dense coastal heath, seasonal stream systems, and winter-wet coastal swamps. Both species flower in spring. Fire is not an essential prerequisite for flowering, but the flowering of both species is promoted by such an event. Dispersal of seed begins 8–12 weeks after pollination. **(DJ)**

Pollination

No detailed studies have been conducted on the pollination of *Elythranthera.* However, the flowers appear to secrete no nectar or odour, and Dafni and Bernhardt (1990) considered them to be food-deceptive mimics of the spring-flowering guild of pink/-purple buzz-pollinated (Buchman 1983) monocot species with poricidal anthers. Both *Elythranthera* species have reduced labella with a pair of prominent, elongated, yellow and purplish black basal calli resembling the poricidal anthers of Hemerocallidaceae and Laxmanniaceae. These calli are attached to either side of the labellum base and can be moved independently of each other and the labellum (George 1963). Dafni and Bernhardt (1990) and Hoffman and Brown (1992) indicated that *Elythranthera* species are pollinated by bees but gave no details. Visiting bees probably seek nonexistent food—pollen from the labellum appendages and nectar from the base of the column. The bright pink and purple coloration and the radially symmetrical perianth are typical of many common food-rewarding species, particularly monocots (Vogel 1978; Bernhardt and Burns-Balogh 1986*a*). **(CCB)**

Uses

Both species of *Elythranthera* are occasionally cultivated as ornamentals by specialist growers. **(DJ)**

Cultivation

Treat as for *Caladenia*. Species are difficult to maintain in cultivation. Propagate from seed sown around parent plants. **(HR)**

Taxonomic literature

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29. ERIOCHILUS

Eriochilus R.Br., *Prodr.*, 323 (1810). Type species: *Eriochilus autumnalis* R.Br., *nom. illeg.*

Derivation of name

From the Greek *erion*, wool, and *cheilos*, lip, alluding to the conspicuous labellum trichomes, which appear woolly. **(DJ)**

Description (Plates 30, 31; Fig. 29.1)

Perennial geophytic *herbs*. *Roots* absent or filamentous. *Tubers* globose, solitary, fleshy, naked; replacement tubers formed at the end of short droppers; daughter tubers absent in most species or rarely) formed on the end of slender root-like stolons. *Stem* erect, short, unbranched, with a membranous cataphyll at the apical node. *Leaf* solitary, basal or perched above ground on an extended petiole which is contiguous with the base of the scape, sometimes undeveloped at anthesis; lamina mostly ovate, subcoriaceous, convolute in bud, glabrous or hairy, margins entire or undulate; venation anastomosing. *Inflorescence* racemose, 1–few flowered, erect, terminal; scape without sterile bracts; floral bracts small, sheathing. *Flowers* resupinate, dull-coloured, pedicellate. *Dorsal sepal* free, smaller than the lateral sepals, strongly cucullate over the column. *Lateral sepals* free, clawed, larger than the dorsal sepal and more conspicuous. *Petals* free, much smaller and narrower than the lateral sepals. *Labellum* free, attached by its base to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina obscurely three-lobed, the basal part closely embracing the ventral surface of the column to form a narrow tube, strongly recurved medially, the mid-lobe broadened, thickened and adorned with clusters of simple, acicular trichomes; callus a slightly raised fleshy plate on the proximal half of the labellum; nectar present. *Column* lacking free filament and style, slender, straight, narrowly winged throughout, a prominent patch of acicular trichomes on the ventral surface; column foot absent; anther terminal, two-celled, persistent, basifixed, erect, papillate, rostrate; hemipollinaria two, each consisting of four pollinia attached directly to a viscidium; pollinia clavate, granular, yellow; viscidium terminal; rostellum ventral, bilobed; stigma entire, transverse, concave. *Ovary* elongate, ribbed, covered with glandular trichomes. *Capsules* dehiscent, glabrous or hairy, erect; pedicels not elongated in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 29.2)

A genus of about 12 species endemic in Australia. **(DJ)**

Palynology

Nothing has been published about pollen ultrastructure of *Eriochilus*. **(AP)**

Ecology

Eriochilus is widely distributed across southern Australia between about 114° and 146° east and latitudinally from about 27° south (north of Kalbarri in Western Australia) and about 25° south on Fraser Island in eastern Australia to about 43° south in Tasmania. All species of *Eriochilus* are terrestrial and grow variously as scattered individuals, in crowded tufts or in clonal colonies. They range from sea level to about 1000 m and occur in areas that have a strong seasonal climate. The majority of species grow actively in autumn and winter, flower in either autumn or spring, and survive the rigours of summer as dormant tubers. Plants of *E. cucullatus* (Labill.) Rchb.f. from subalpine regions in south-eastern Australia, however, commonly grow and flower over summer.

Eriochilus plants occur in a wide range of habitats including open forest, woodland, shrubland, heathy forests, coastal scrubs, heathland, granite outcrops, salt-lake margins, and winter-wet swamps.

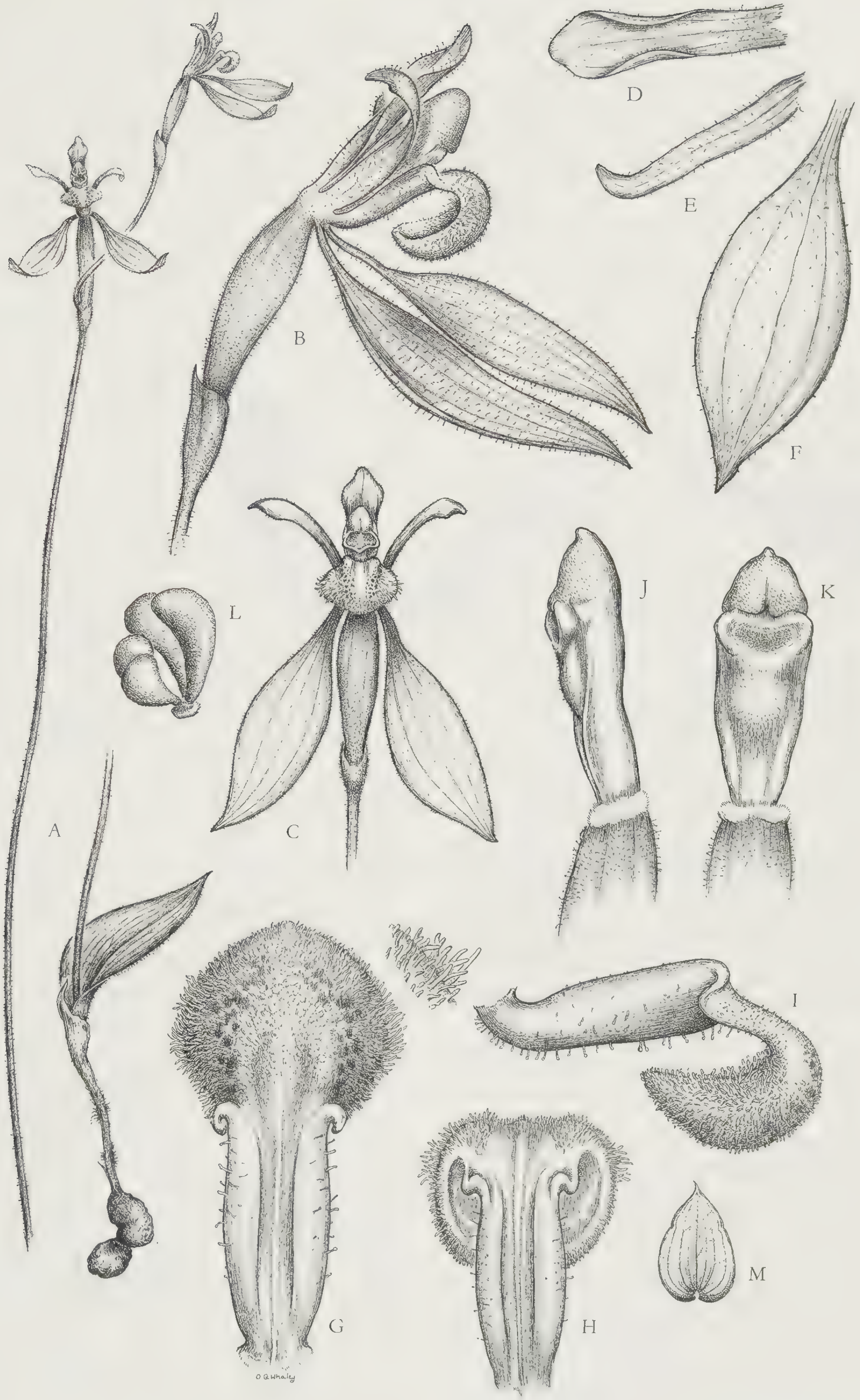

Fig. 29.1. *Eriochilus cucullatus* (Labill.) Rchb.f. A. Habit, ×1; B. Flower from side, ×6; C. Flower from front, ×4.5; D. Dorsal sepal, ×6; E. Petal, ×6; F. Lateral sepal, ×6; G. Labellum flattened, from above, ×12; H. Labellum from above, ×12; I. Labellum from side, ×9; J. Column from side, ×9; K. Column from front, ×9; L. Hemipollinarium, ×15; M. Leaf, ×1. Drawn by Oliver Q. Whalley from Kew Spirit Collection nos. 55512 and 36875.

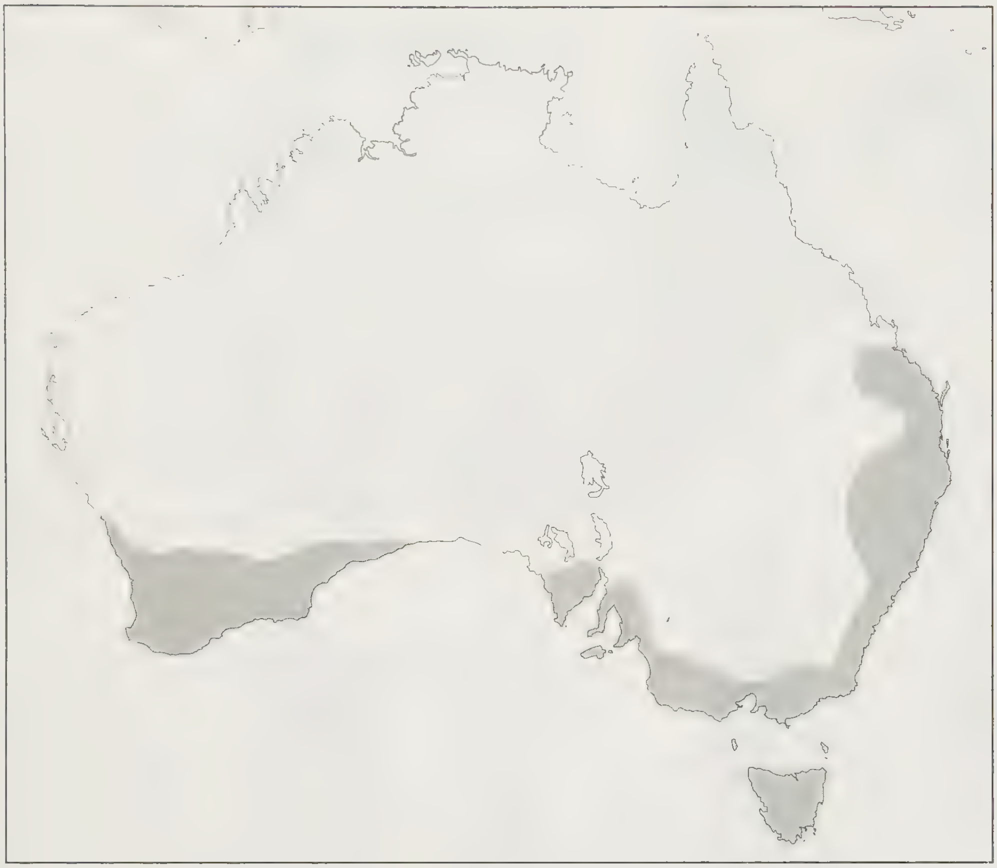

Fig. 29.2. Distribution map of *Eriochilus*.

Flowering in overgrown habitats is greatly reduced, and all species are generally enhanced by the occurrence of summer fires. Two colony-forming species, *E. scaber* Lindl. and *E. tenuis* Lindl., both from Western Australia, flower in mass after hot summer fires and rarely in unburnt habitat. Dispersal of seed begins 8–16 weeks after pollination. **(DJ)**

Pollination

No formal scientific studies of the pollination of *Eriochilus* have been undertaken. However, reports by naturalists indicate some species are pollinated by native bees. Erickson (1965) reported the capture of *Hylaeus dorothiae* (Colletidae) on a flower of the Western Australian *E. dilatatus* subsp. *undulatus* (Hoffman and Brown 1992), and at least two species of *Halictus* (Halictidae) have been observed pollinating *E. cucullatus* in South Australia (Bates 1987). Peakall (personal communication) observed native bees of the genus *Lasioglossum* (Halictidae) visiting flowers of *E. multiflorus* Lindl. in Western Australia. The flowers of *Eriochilus* species are remarkably similar, indicating that the same pollination mechanism may apply across the whole genus.

Eriochilus has several features characteristic of bee-pollinated flowers. The prominent pink or white sepals, although only two in number, radiate from the centre of the flower, guiding pollinators to the densely woolly labellum. The flowers of at least some species have a sweet odour, and some are also reported to secrete nectar. A faint honey-like perfume is emitted from *E. cucullatus* on warm autumn days (Bates 1987; C. Bower, unpublished), and *E. multiflorus* (R. Peakall, personal communication), and *E. scaber* (Bates 1986*b*) may produce strong sweet odours.

An abundant, clear, sticky, nectar-like substance accumulates in the narrow space between the bases of the labellum and column of *E. cucullatus* (D. Jones, personal communication; C. Bower, unpublished), although Bates (1987) could find little in flowers he examined. Nectar is also provided by *E. scaber* (Bates 1986*b*). *Eriochilus* therefore appears to be one of the few genera of Diurideae that rewards pollinators, although confirmation is needed. This conclusion contradicts that of Dafni and Bernhardt (1990), who classified *Eriochilus* as food mimics on the basis of Erickson's (1965) report. Dafni and Bernhardt (1990) postulated that the labellum hairs of *Eriochilus* represented pseudostamens.

The pollination mechanism of *Eriochilus* differs from that of other Caladeniinae in a number of ways. The stigma is unique, having a deep cavity with a narrow opening. The inner surface is exceedingly viscous and the margins of the opening flexible, so that it can be readily enlarged by pulling them outward or downward. Also unique is the presence of a pair of slots in the upper edge of the stigma that holds two removable viscidia representing the rostellum. These face downward in the upper horizontal surface of the stigma. The four pollinia in each of the anther cells are directly attached to one of the viscidia through the slot. Each anther cell and its pollinia are covered by an anther cap similar to those found in other Caladeniinae. Medial extensions of each cap cover the outer edges of the slots and the edges of the viscidia.

Bees land on the horizontal portion of the labellum and push their heads into the narrow gap between the labellum and column (Bates 1987). The labellum base is thick, straight, and U-shaped in cross section, forming a narrow tube with the column. It is rigidly attached and immobile so that bees cannot penetrate the tube. The insect requires a long tongue and must push its head as deeply as possible into the orifice (which enlarges the opening to the stigma by pulling down its flexible lower margin) to reach the nectar (Erickson 1965). The pollinia, which are carried on the frons, are thrust into the stigmatic cavity and held by the sticky surface. As the bee retreats the pollinia break from the viscidia at their narrow connections. This may be aided by the closure of the opening around the cavity and the pollinia (Erickson 1965).

The top of the bee's frons then lifts the anther flaps, which were held closed on entry, and contacts the upper margin of the stigma and the edges of one or both viscidia. Upward stretching of the flexible stigma is likely to increase contact with the viscidia, the main surfaces of which lie within the stigmatic cavity (C. Bower, unpublished). These adhere to the frons and are pulled free (Plate 31). Erickson (1965) contends that as they leave the anther the pollinia are bent by the flaps into a position suitable for insertion into the stigma of another flower. However, microscopic examination shows that the pollinia are already in the correct orientation before they are removed (C. Bower, unpublished). It is likely Erickson (1965) was unaware of the position of the viscidia within the stigmatic cavity and had only seen their outer edges.

The minimal data available indicate that, in common with other food-rewarding orchids, quite high percentages of flowers may be pollinated. Erickson (1965) reported that 40 out of 42 flowers of *E. multiflorus* subsp. *dilatatus* were pollinated in one colony. Bates (1987) reported levels of 10% and 50% in shaded and unshaded flowers of *E. cucullatus*, respectively.

Eriochilus species tend to flower when competition for pollinators from other species is minimal. Many taxa bloom in late summer, autumn, or early winter when few other plants are in flower. Spring-flowering Western Australian species flower mainly after fires in the previous summer, when most other flowering plants have been severely reduced in abundance. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Mix: basic with extra coarse sand or other drainage material. Light: 50% shade. Watering: keep moist from early autumn for autumn-flowering species until late spring. Flowering: well-grown autumn-flowering species flower easily. However, the winter–spring flowering species from Western Australia rarely flower in the wild except after hot summer fires. Flowering for these may be induced by storing tubers with a banana skin for two weeks during the dormant period before replanting them. Propagation: most are solitary, but winter–spring flowering species are colony-formers. Solitary species can be propagated by tuber removal or spreading seed around parent plants. **(HR)**

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30. GLOSSODIA

Glossodia R.Br., *Prodr.*, 325 (1810). Type species: *Glossodia major* R.Br.

Glossodia R.Br. sect. *Eu-Glossodia* Endl., *Nov. Stirp. Dec.*, **2**, 16 (1839).

Derivation of name

From the Greek *glossa*, tongue, and *-odes*, likeness, apparently referring to the tongue-like or strap-shaped calli at the labellum base. **(DJ)**

Description (Plate 32; Fig. 30.1)

Perennial geophytic *herbs*. *Roots* absent. *Tubers* globose, paired, fleshy, enclosed fully within a multi-layered persistent fibrous tunic;

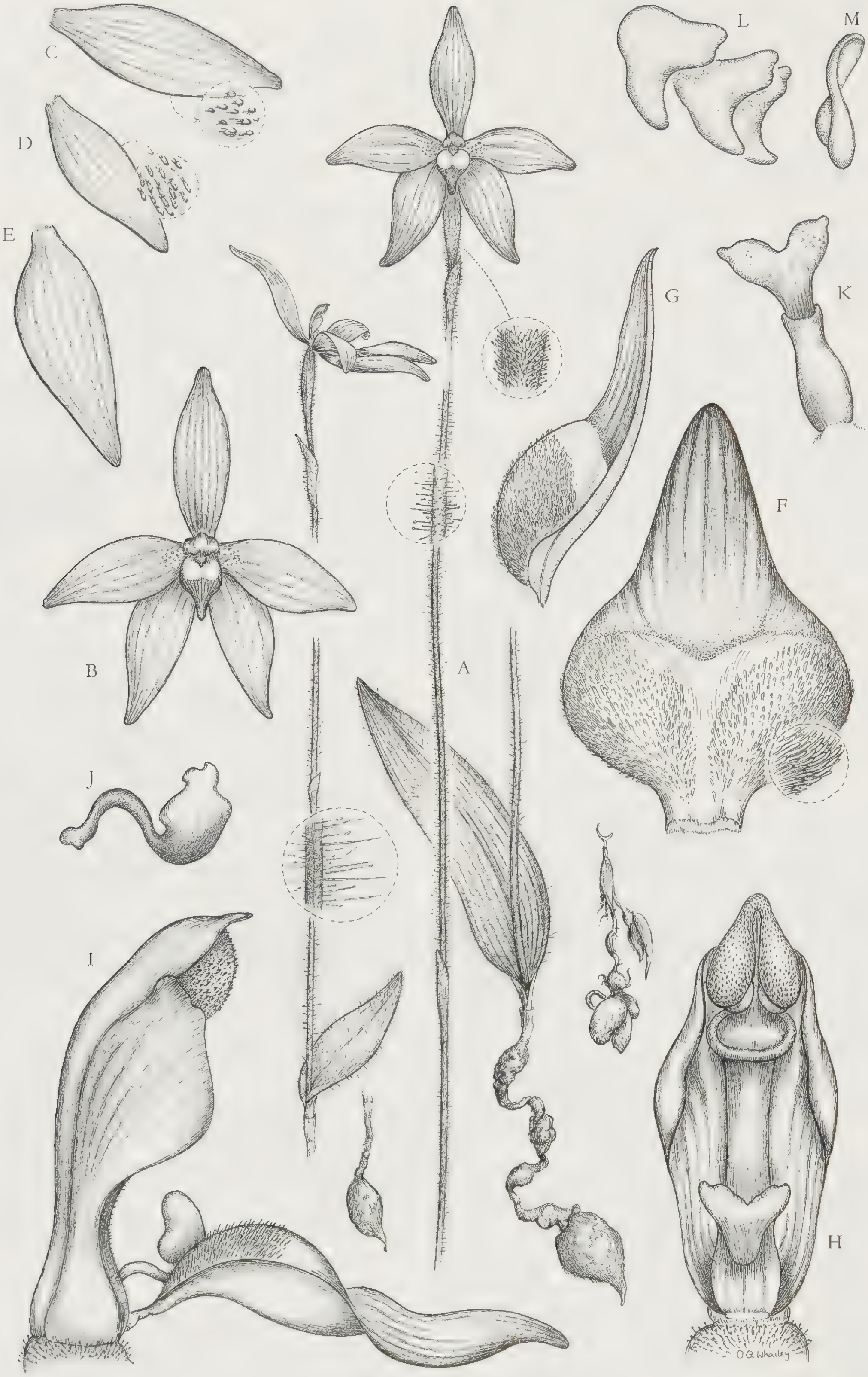

Fig. 30.1. *Glossodia major* R.Br. A. Habit, ×1 (scape hairs, ×3; ovary hairs, ×6); B. Flower from front, ×1.5; C. Dorsal sepal, ×1.5 (hairs, ×30); D. Petal, ×1.5 (hairs, ×30); E. Lateral sepal, ×1.5; F. Labellum from above (calli enlarged), ×9; G. Labellum, longitudinal section, ×9; H. Column from front, ×9; I. Column and labellum from side, ×9; J. Labellum gland/fused calli from side, ×9; K. Labellum gland/fused calli from above, ×9; L. Pollinia, ×9; M. Pollinium from side, ×9. Drawn by Oliver Q. Whalley.

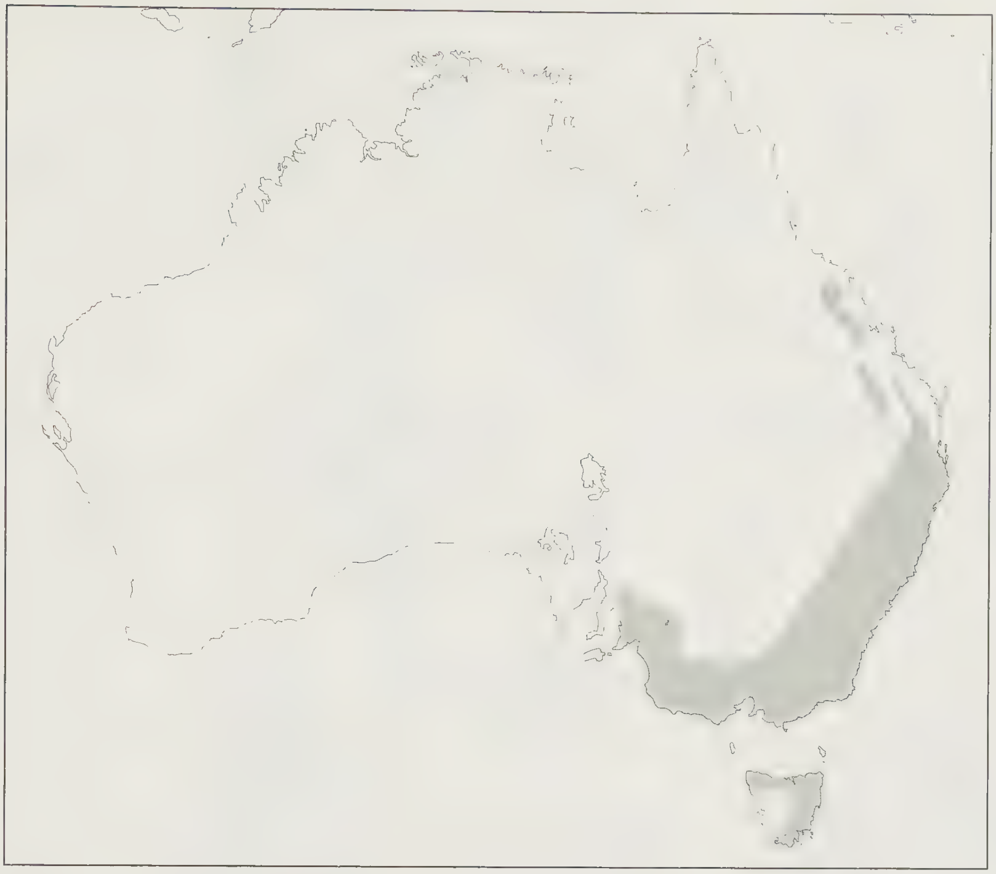

Fig. 30.2. Distribution map of *Glossodia.*

replacement tubers formed within the tunic on the end of short droppers; daughter tubers absent. *Stem* erect, short, unbranched, with a membranous cataphyll at the apical node, covered by a multi-layered persistent fibrous tunic to the soil surface. *Leaf* solitary, basal, sessile, hairy; lamina mostly lanceolate, subcoriaceous, convolute in bud, margins entire; venation anastomosing. *Inflorescence* racemose, 1 (2)flowered, erect, terminal; scape with one sterile bract; floral bracts foliaceous, sheathing. *Flowers* resupinate, brightly coloured, pedicellate. Sepals and petals subsimilar, glandular externally. *Dorsal sepal* free, spreading. *Lateral sepals* free, porrect. *Petals* free. *Labellum* free, attached by its base to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina obscurely three-lobed, the lateral lobes fleshy, papillate, the margins spreading, entire; callus reduced to one or two basal calli, swollen, not ornamented, on a flattened, curved claw; nectar absent. *Column* lacking free filament and style, straight, broadly winged, the wings translucent and expansive distally; column foot absent; anther terminal, four-celled, persistent, basifixed, erect, papillate, rostrate; pollinia four, lobed, flat, mealy, naked, cream to pale yellow; rostellum ventral; stigma entire, circular, concave. *Ovary* elongate, ribbed, covered with glandular trichomes. *Capsules* dehiscent, hairy, erect; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 30.2)

A genus of two species endemic in southern and eastern Australia. **(DJ)**

Palynology

Nothing has been published about pollen ultrastructure of *Glossodia.* **(AP)**

Ecology

Glossodia major, one of the commonest orchids of south-eastern Australia, is distributed from the coast to about 250 km inland between Dick's Tableland near Mackay (21° south) and 43° south in southern Tasmania. It ranges from the coastal lowlands up to about 800 m in the mountains and grows in a wide range of habitats including sclerophyll forest and woodland, shrubland, heathy forest, heathland, and coastal scrubs, always in well-drained soils. By contrast, *G. minor* R.Br. is restricted to lowland coastal and near-coastal districts growing mainly in heath and heathy forest. Both species flower in spring. Fire is not an essential prerequisite for flowering, but flowering is enhanced in both species following such an event. Reproduction is solely from seed with dispersal beginning 8–12 weeks after pollination. **(DJ)**

Pollination

Despite the abundance and widespread distribution of *Glossodia* species, nothing appears to have been recorded of the pollination mechanisms or pollinators. Cady and Rotherham (1970) considered *Glossodia* flowers to be adapted for insect pollination because of the occurrence of intergeneric hybrids with some species of *Caladenia* section *Caladenia* and an anther structure unsuited to self-pollination. Other factors indicating insect pollination are the freely opening flowers, the brightly coloured, radially symmetrical tepals, and the column appendages, which like the labellum appendages of *Elythranthera* appear to be anther mimics.

On the other hand, flowers of *Glossodia* appear to secrete no nectar and lack scent. The most likely pollination mechanism is food deception with native bees as the most probable pollinators. As in *Elythranthera*, the labellum of both *Glossodia* species is reduced and the appendages purplish black and/or yellow. The dark, divided appendage of *G. minor* is similar to the anthers of buzz-pollinated flowers in *Solanum* (Solanaceae) and some monocot families (e.g. Hemerocallidaceae and Laxmanniaceae) but provides no pollen. The double-headed yellow appendage of *G. major*, on the other hand, appears to mimic a pollen-covered anther. Jones (unpublished) observed small native bees removing pollinia from *G. major* while attempting to remove pollen from the labellum appendages. **(CCB)**

Uses

Both species are occasionally grown as ornamentals by specialist growers. **(DJ)**

Cultivation

Treat as for *Caladenia*. *Glossodia* species are difficult to maintain in cultivation for long periods of time, and every effort needs to be made to propagate them from seed sprinkled around parent plants. **(HR)**

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31. LEPTOCERAS

Leptoceras (R.Br.) Lindl., *Edward's Bot. Reg.*, 1–23: *Swan Riv. Append.*, liii (1840). Type species: *Caladenia menziesii* R.Br. (*Leptoceras menziesii* (R.Br.) Lindl.).

Caladenia R.Br. sect. *Leptoceras* R.Br., *Prodr.*, 325 (1810). Type species: *Caladenia menziesii* R.Br.

Derivation of name

From the Greek *leptos*, slender, and *keras*, horn, referring to the erect petals that resemble horns. **(DJ)**

Description (Plate 33; Fig. 31.1)

Perennial geophytic *herbs*. *Roots* filamentous. *Tubers* globose, paired, fleshy, partly enclosed within a multi-layered persistent fibrous tunic; replacement tubers formed at the end of short droppers; daughter tubers formed on the end of slender root-like stolons. *Stem* erect, short, unbranched, with a membranous cataphyll at the apical node, covered by a multi-layered persistent fibrous tunic to the soil surface. *Leaf* solitary, basal, sessile, glabrous or with a few trichomes; lamina ovate, subcoriaceous, convolute in bud, margins entire, a small ligule-like growth in the base of sterile leaves; venation anastomosing. *Inflorescence* racemose, 1–few flowered, erect, terminal; scape hairy, with one sterile bract; floral bracts foliaceous, sheathing. *Flowers* resupinate, dull-coloured, pedicellate; perianth glandular externally. *Dorsal sepal* free, dissimilar to the lateral sepals, cucullate over the column. *Lateral sepals* free, erect. *Petals* free, erect, clavate, densely glandular, markedly dissimilar in size and shape to the sepals. *Labellum* free, attached by its base to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina obscurely three-lobed, the margins erect, entire or slightly irregular; callus of two irregular longitudinal rows of calli; calli stalked, gammate, papillate; basal calli similar to the rest; nectar present. *Column* lacking free filament and style, incurved or nearly straight, broadly winged; column foot absent; anther terminal, four-celled, persistent, basifixed, erect, papillate, rostrate; pollinia four, bilobed, flat, mealy, naked, yellow; rostellum ventral; stigma entire, circular, concave. *Ovary* elongate, ribbed, covered with glandular trichomes. *Capsules* dehiscent, hairy, erect; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

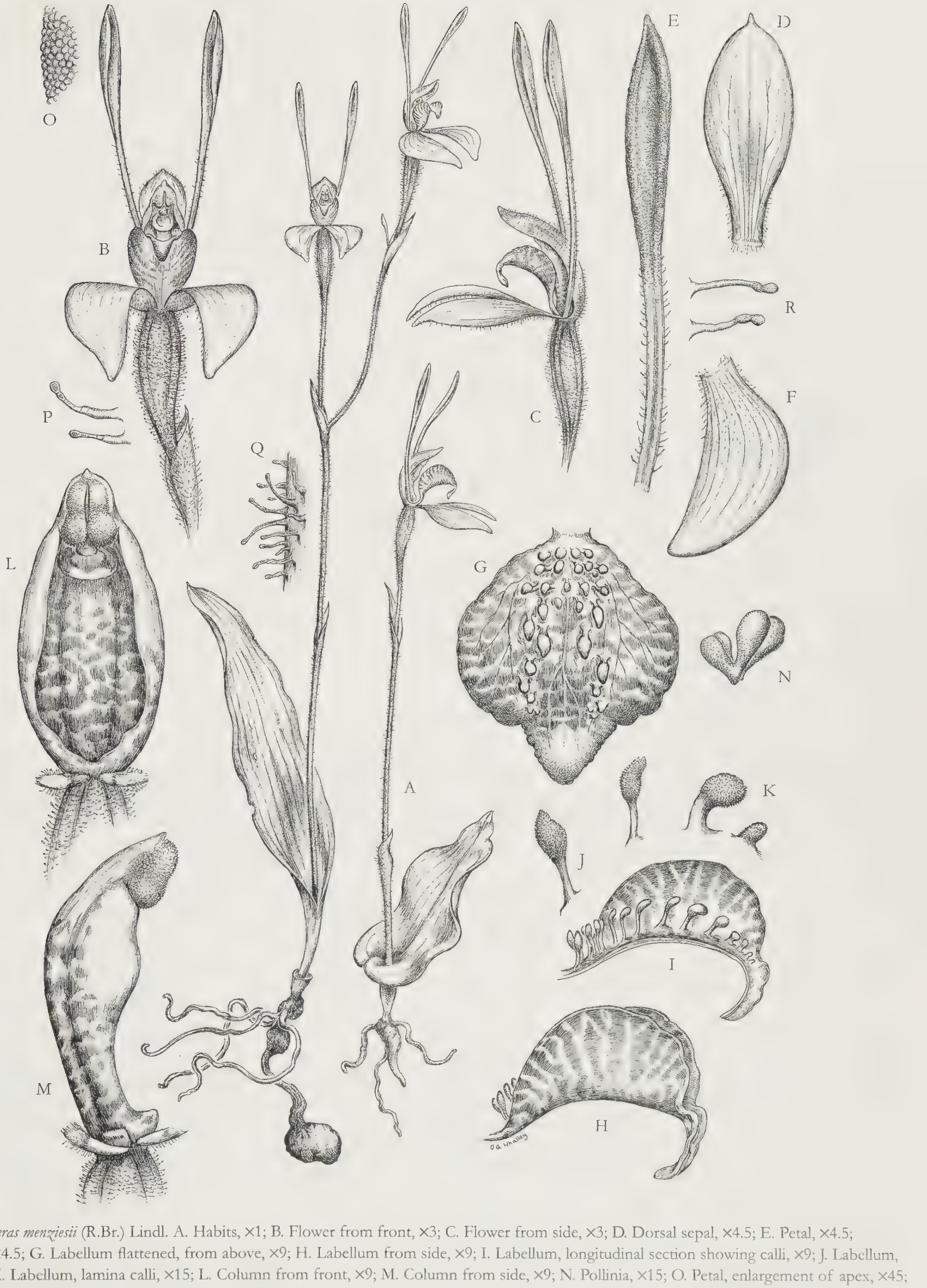

Fig. 31.1. *Leptoceras menziesii* (R.Br.) Lindl. A. Habits, ×1; B. Flower from front, ×3; C. Flower from side, ×3; D. Dorsal sepal, ×4.5; E. Petal, ×4.5; F. Lateral sepal, ×4.5; G. Labellum flattened, from above, ×9; H. Labellum from side, ×9; I. Labellum, longitudinal section showing calli, ×9; J. Labellum, basal calli, ×15; K. Labellum, lamina calli, ×15; L. Column from front, ×9; M. Column from side, ×9; N. Pollinia, ×15; O. Petal, enlargement of apex, ×45; P. Ovary, hairs, ×45; Q. Stem, hairs, ×21; R. Petal, basal hairs, ×45. Drawn by Oliver Q. Whalley from Kew Spirit Collection no. 47027.

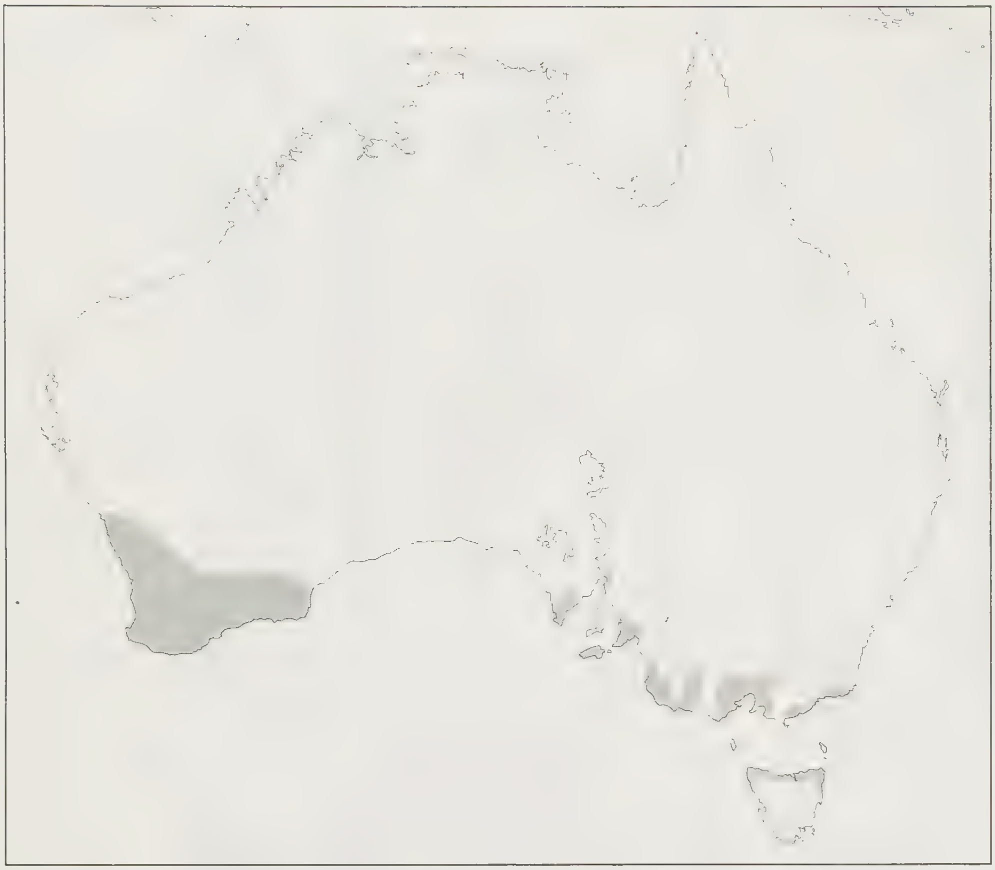

Fig. 31.2. Distribution map of *Leptoceras.*

Distribution (Fig. 31.2)

A monospecific genus endemic in southern and western Australia. **(DJ)**

Palynology

Nothing has been published about pollen ultrastructure of *Leptoceras.* **(AP)**

Ecology

Leptoceras menziesii is widely distributed across lowland areas of southern and western Australia between about 115°–121° east. In Western Australia it ranges between about 27° south near Kalbarri to about 35° south on the south coast, whereas in eastern Australia it has a more restricted latitudinal range between about 36°30′–41°20′. This species reproduces freely by vegetative means to form dense colonies that may be extensive. It is common in coastal and near-coastal heathlands and heathy forests, but it also extends inland, especially in Western Australia, growing in sclerophyll forests, woodland, shrubland, and on large granite outcrops. It also colonizes *Pinus radiata* D. Don plantations in South Australia. Soil drainage is usually unimpeded, but in Western Australia the species is often found in winter-wet swamps. Flowering is greatly enhanced by summer fires, to such an extent that it is common for massed displays to occur the following spring, especially when there have been long intervals between burns. Dispersal of seed begins 8–12 weeks after pollination. **(DJ)**

Pollination

Scientific studies on the pollination of *L. menziesii* are lacking, and anecdotal accounts in the literature are contradictory. Both Jones (1988) and Backhouse and Jeanes (1995) indicated that *L. menziesii* has a sweet fragrance. By contrast, Bates (1985*b*) said that no perfume is apparent, but Bates and Weber (1990) stated that flowers may or may not be lightly scented. Similarly, Hoffman and Brown (1992) and D. Jones (personal communication) reported that small droplets of nectar are present at the base of the column, but Bates (1985*b*) stated that no food reward is provided. It may be that populations vary in the presence of fragrance and nectar over the large range of this species.

Bates (1985*b*), Bates and Weber (1990), and Hoffman and Brown (1992) all stated that *L. menziesii* is bee-pollinated. However, in no case is the species of bee identified. The flowers certainly have features characteristic of plants pollinated by bees, particularly the bright white lateral sepals and the floral tube formed between the labellum, with its upturned side lobes, and the column. The central lamina of the labellum has two to four rows of stalked yellow calli that may mimic pollen-bearing stamens. Hoffman and Brown (1992) hypothesized that the dark-coloured erect petals may be anther mimics.

Bates (1985*b*) has made the only detailed observations of pollination of *L. menziesii*. On a warm sunny day near Albany in Western Perth, Australia, tiny native bees were seen working the flowers of a pink daisy, *Lagenophora huegelii*. Some of the bees bore orchid pollinia on the thorax and were occasionally seen visiting flowers of *L. menziesii* growing among the *Lagenophora*. The bees landed on the apex of the orchid labellum and quickly moved into the tube where they appeared to examine the calli. Incoming pollinia were deposited on the stigma, and 'in the same movement' new pollinia were collected from the anther. Over 50% of bee visits to *L. menziesii* resulted in removal of pollinia and up to 60% of flowers set capsules.

Bates (1985*b*) interpreted the occasional short visits of bees to *L. menziesii* as evidence the flowers were unrewarding and that *L. menziesii* therefore employs a 'vague floral mimicry'. Further work is needed to determine the significance of reports of the presence of nectar and odour in some populations of *L. menziesii*. **(CCB)**

Uses

Leptoceras is rarely cultivated as an ornamental by specialist growers. **(DJ)**

Cultivation

Mix: basic with extra coarse sand for good drainage. Light: 50% shade. Watering: keep moist from early autumn to late spring. Flowering: a notoriously poor flowerer in cultivation and a species that flowers in the wild after a hot summer fire. Flowering can be induced in cultivation by storing the tubers with a banana skin for two weeks during the dormant stage before replanting. Propagation: colony-former, with multiplication rate ×2 on average. **(HR)**

Taxonomic literature

Backhouse, G. and Jeanes, J. (1995). *The orchids of Victoria*. Miegunyah Press, Carlton, Victoria.

Bishop, T. (1996). *Field guide to the orchids of New South Wales and Victoria*. University of New South Wales Press, Sydney.

Hoffman, N. and Brown, A. P. (1992). *Orchids of south-west Australia*. University of Western Australia Press, Nedlands.

Walsh, N. G. and Entwisle, T. J. (1994). *Flora of Victoria*, Vol. 2. Inkata Press, Melbourne.

32. PRAECOXANTHUS

Praecoxanthus Hopper & A. P. Brown, *Lindleyana*, **15**, 124. Type species: *Caladenia aphylla* Benth. (*Praecoxanthus aphyllus* (Benth.) Hopper & A. P. Browne).

Derivation of name

From the Latin *praecox*, precocious, developing early, and Greek *anthos*, flower, alluding to the autumnal flowering habit of this orchid. **(DJ)**

Description (Plate 34; Fig. 32.1)

Perennial geophytic *herbs*, sympodial. *Roots* filamentous. *Tubers* globose, paired, fleshy, partly enclosed within a multi-layered persistent fibrous tunic; replacement tuber formed at the end of a short dropper; daughter tubers absent. *Stem* erect, short, unbranched, with a membranous cataphyll at the apical node, covered by a multi-layered persistent fibrous tunic to the soil surface. *Trichomes* absent on most parts. *Leaf* of non-flowering plants solitary, sessile, with prominent white veins; lamina ovate to obovate, convolute in bud, glabrous, margins entire; venation anastomosing. *Leaf* of flowering plants reduced to a sheathing bract-like structure. *Inflorescence* one flowered, erect, terminal; scape wiry, glabrous, with one sterile bract; floral bract reduced, sheathing. *Flowers* resupinate, dull-coloured, pedicellate, fragrant; perianth externally glandular, with trichomes similar to those on the ovary. *Dorsal sepal* free, similar to the lateral sepals, spreading to recurved. *Lateral sepals* free. *Petals* free, subsimilar to the lateral sepals. *Labellum* free, attached by a short claw to the anterior column base, markedly dissimilar in size, shape and colour to the sepals and petals, ecalcarate; lamina strongly three lobed, the margins erect and incurved, entire; callus of two irregular longitudinal rows of calli, the calli stalked, clavate, straight or curved, papillate, the basal calli hardly different from the rest; nectar absent. *Column* lacking free filament and style, slender, incurved, narrowly winged, the wings expansive distally; column foot absent; anther terminal, four-celled, persistent, basifixed, erect, papillate, rostrate; pollinia four, bilobed, flat, mealy, naked, yellow; rostellum ventral; stigma entire, circular, concave. *Ovary* elongate, ribbed, with sparse trichomes. *Capsules* dehiscent, hairy, erect; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 32.2)

A monospecific genus endemic in south-western Western Australia. **(DJ)**

Palynology

Nothing has been published about pollen ultrastructure of *Praecoxanthus*. **(AP)**

Ecology

Praecoxanthus aphyllus occurs between about 32°30′–35° south and grows in heathland, heathy woodland, and shrubby woodland dominated by species of *Banksia*, *Allocasuarina*, and *Eucalyptus*. Soils are mainly well-drained sand or lateritic gravels. Flowering occurs in the autumn months of March to May. The species reproduces solely from seed, which begins to disperse 8–12 weeks after pollination. **(DJ)**

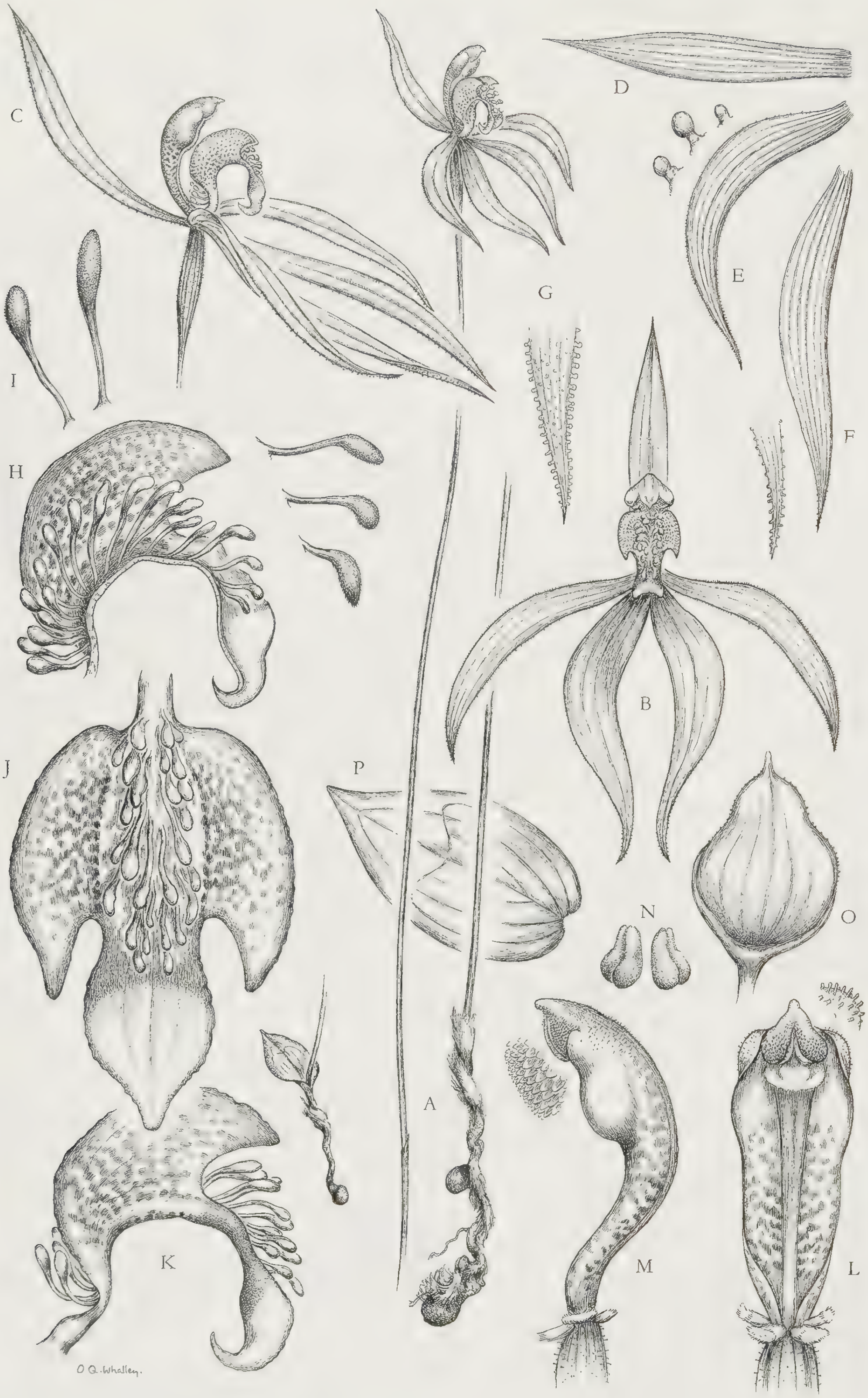

Fig. 32.1. *Praecoxanthus aphyllus* (Benth.) Hopper & A. P. Br. A. Habit, ×1; B. Flower from front, ×3; C. Flower from side, ×3; D. Dorsal sepal, ×3; E. Petal, ×3; F. Lateral sepal, ×3; G. Petal enlargement, ×15; H. Labellum, longitudinal section, ×9; I. Labellum calli, ×15; J. Labellum flattened out, from above, ×9; K. Labellum from side, ×9; L. Column from front, ×6; M. Column from side, ×6; N. Pollinia, ×9; O. Floral bract, ×6; P. Leaf (from sterile plant), ×4.5. Drawn by Oliver Q. Whalley from *Morrison s.n.* (K).

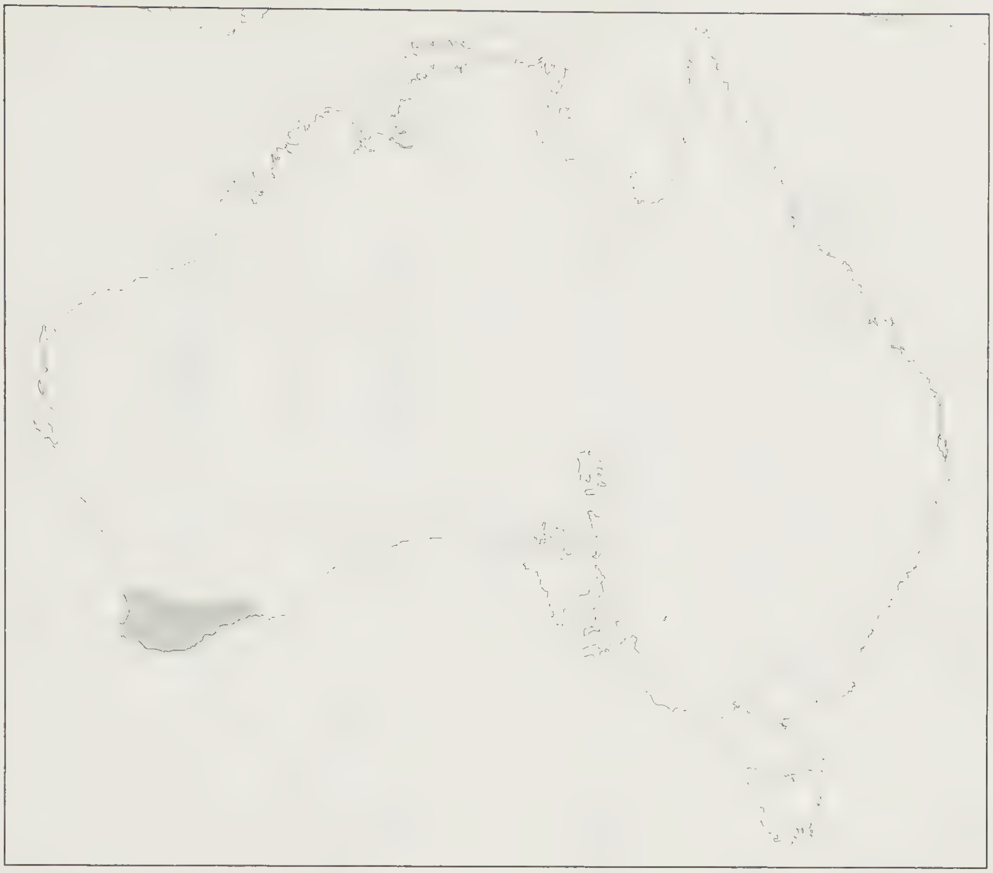

Fig. 32.2. Distribution map of *Praecoxanthus*.

Pollination

The pollinator of *Praecoxanthus aphyllus* is unknown. However, many features of the flower indicate it is pollinated by native bees or other insects seeking nectar or pollen. A strong fragrance is emitted (Hoffman and Brown 1992), which would normally advertise the presence of nectar to bees, but there is none (D. L. Jones, unpublished). The radiating bright yellow-and-white perianth segments also indicate food, whereas the colourful yellow-and-purple labellum apex may be a generalized mimic of the anthers of monocot taxa. The prominent yellow-headed calli of the labellum may also be mimics of pollen-covered stamens. Prominent lateral lobes of the labellum and column wings form a floral tube down which an insect may move in search of nectar at the base of the column. **(CCB)**

Uses

None reported. **(DJ)**

Cultivation

Treat as for *Caladenia*. **(HR)**

Taxonomic literature

Hoffman, N. and Brown, A. P. (1992). *Orchids of south-west Australia*. University of Western Australia Press, Nedlands.

SUBTRIBE CRYPTOSTYLIDINAE

Cryptostylidinae Schltr., *Bot. Jahrb. Syst.*, **45**, 381 (1911). Type: *Cryptostylis* R.Br.

Description

Glabrous, geophytic *herbs*. *Tubers* absent, the roots long and fleshy. *Leaf* absent or 1 or more per shoot, convolute, longer than wide, erect, coriaceous, petiolate. Inflorescence racemose. *Flowers* non-resupinate, dull-coloured; tepals subsimilar. *Labellum* fixed to the base of the column, often much larger than the tepals; lamina glabrous or hirsute, with or without calli, nectar absent. *Column* short, lacking free filament and style; column foot absent; pollinarium present; pollinia four. *Fruit* a dehiscent capsule. **(DJ)**

Anatomy

Leaf

SURFACE

Hairs absent. Epidermis: cells polygonal to axially elongated and rectangular or elliptical; walls thin, pit-fields not conspicuous.

Stomata on abaxial surface only. Guard cells in *Coilochilus* with pigment or mucilage droplets.

TRANSECTION

Cuticle thin (*Cryptostylis*) or thick (*Coilochilus*), depending on species, papillate to striate. Epidermis: cells elliptical to rectangular, often anticlinally oriented abaxially; outer wall thickened. Stomata superficial, substomatal chambers shallow. Mesophyll homogeneous in *Coilochilus*, heterogeneous (1–3 layered palisade) in *Cryptostylis*. Vascular bundles as for the tribe. Bundle-sheath 1–3 layered, cells thin-walled. Crystals: raphides in mesophyll idioblasts.

Stem

TRANSECTION

Hairs absent. Cuticle thin, smooth to slightly papillose. Epidermis: cells elliptical, rectangular to polygonal, outer wall thickened. Stomata absent. Cortex: outer layers parenchymatous, inner layers in *C. subulata* (Labill.) Rchb.f. sclerotic forming a sclerenchyma sheath. Ground tissue parenchymatous. Vascular bundles collateral, in two rings. Ergastic substances: none observed.

Root

TRANSECTION/LONGITUDINAL SECTION

Hairs unicellular. Velamen one-layered (*Coilochilus*) or 2–3 layered (*Cryptostylis*), cells elliptical to anticlinally rectangular, with minute pores in *Coilochilus*; walls of uniform thickness. Tilosomes present in *Cryptostylis*. Exodermis: cells square to anticlinally rectangular, outer and radial walls thickened. Cortex parenchymatous, infected with hyphae and pelotons. Endodermis: cells elliptical. Stele medullated, 8–11 arch. Xylem tracheids with helical thickenings, vessel members with scalariform perforation plates. Ergastic substances: cruciate starch grains and raphide bundles throughout cortex. Spiranthosomes absent. **(AP)**

Palynology

Nothing has been published about the pollen ultrastructure of *Cryptostylis* or *Coilochilus*. **(AP)**

Phytochemistry

Phytochemical studies in Cryptostylidinae are limited to *Cryptostylis* (see separate entry). **(NV, RG)**

Phylogenetics

Schlechter (1926) defined Cryptostylidinae as those taxa with radical, single petiolate leaves; slender scape invested with distant bracts; a lax or dense, few or many flowered raceme, and superior labellum, clasping or blocking the small column. He included *Coilochilus* and *Cryptostylis* within the subtribe. There has been substantial disagreement about the position of this subtribe since its publication. Dressler (1974), for example, treated it within Cranchideae, composed predominantly of American genera, moving it later to his subfamily Spiranthoideae (Dressler 1981) and finally into Diurideae (Dressler 1993).

Clements (1995) established the true nature of the relationship of this taxon within Diurideae when by embryological studies it was shown that these two groups shared a common embryo developmental pattern, now termed the diurid pattern (Clements 1999). More recently, results of molecular analyses using the plastid gene *rbcL* (Kores *et al.* 1997) and *matK* (Kores *et al.* 2000) and ITS sequences of nuclear rDNA (Clements *et al.*, in preparation) have confirmed that the Cryptostylidinae, despite the unusual appearance of *Cryptostylis*, do in fact fall entirely within Diurideae, although the exact alignment with other taxa has yet fully to be determined. Clements *et al.* (in preparation) have, however, shown that the presumed alignment of *Coilochilus* within Cryptostylidinae seems artificial, and further research is underway to confirm this result. **(MAC)**

Key to the genera of Cryptostylidinae (DJ)

1. • Roots verrucose; fibrous cataphylls present around petiole base; flowers tiny (less than 2 mm long); labellum of similar size to the other perianth parts . . . .**33. *Coilochilus***
   • Roots smooth; cataphylls membranous; flowers large (more than 15 mm long); labellum much larger than the other parts . . . .**34. *Cryptostylis***

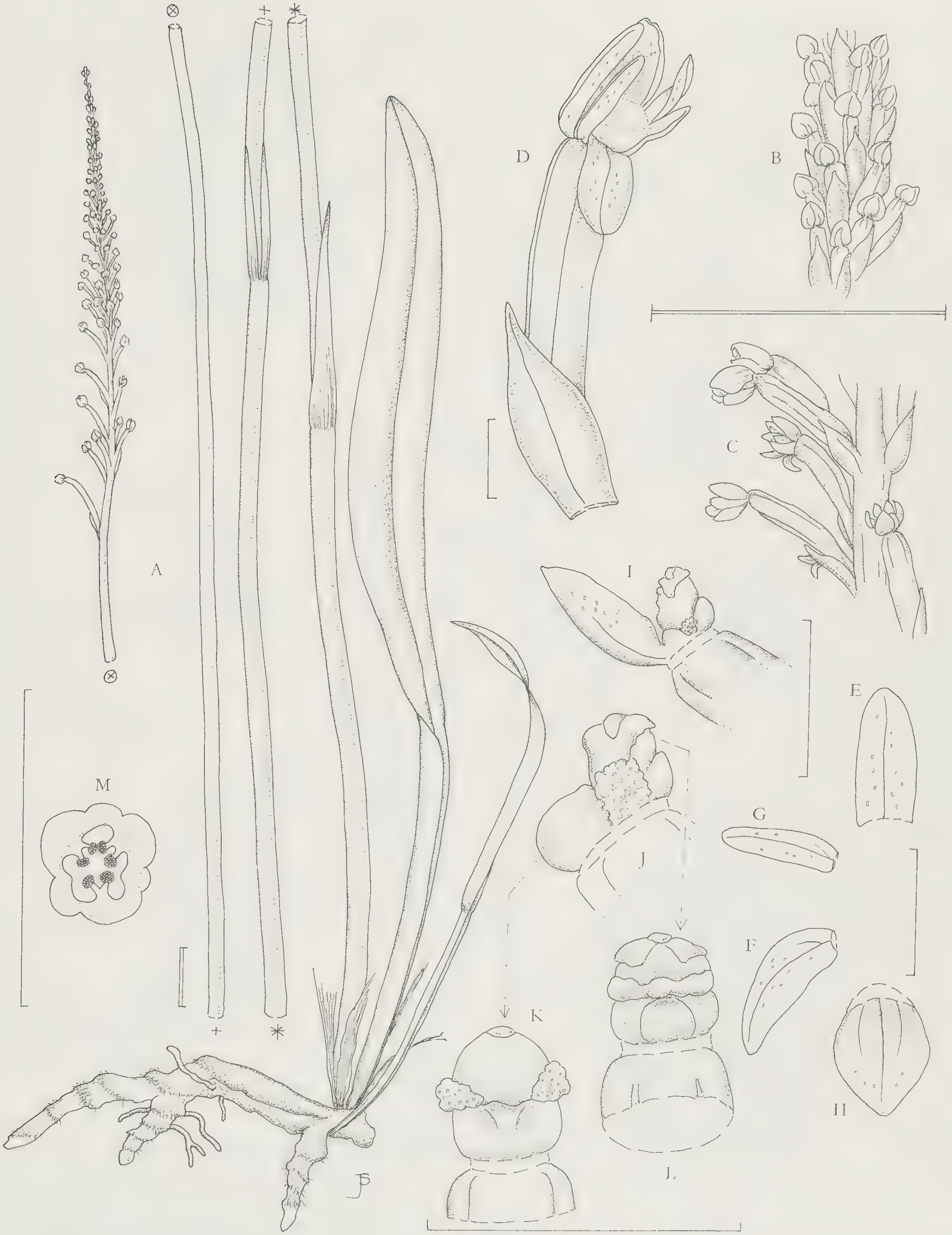

Fig. 33.1. *Coilochilus neocaledonicus* Schltr. A. Habit; B. Inflorescence, apical portion; C. Inflorescence, basal portion; D. Flower; E. Dorsal sepal; F. Lateral sepal; G. Petal; H. Labellum; I. Labellum and column, side view; J. Column, side view; K. Column, front view; L. Column, back view; M. Ovary, transverse section. Single bar = 1 mm; double bar = 1 cm. Drawn by Judi Stone from *McKee 36943* (K) and Kew Spirit Collection no. 54226.

33. COILOCHILUS

Coilochilus Schltr., *Bot. Jahrb.*, **39**, 36 (1906) *et* **45**, 385 (1911).
Type species: *Coilochilus neocaledonicus* Schltr.

Derivation of name

From the Greek *koilos*, hollow, and *cheilos*, lip, referring to the concave labellum. **(DJ)**

Description (Plate 35; Fig. 33.1)

Perennial geophytic *herbs*. *Stem* short, subterranean, persistent, vertical, unbranched, with prominent scarious cataphylls at each node, these persisting at the stem apex. *Roots* thick and fleshy, verrucose. *Tubers* absent. *Leaves* one per shoot, basal, petiolate; lamina much longer than wide, erect, convolute in bud, margins entire; venation anastomosing. *Inflorescence* racemose, many flowered, erect, terminal; scape wiry, with 2–3 sterile bracts; bracts much reduced, sheathing. *Flowers* non-resupinate, tiny, dull-coloured, shortly petiolate; perianth much reduced and inconspicuous. *Sepals* free, subsimilar, narrow. *Petals* free, subsimilar to the sepals. *Labellum* free, attached by its base to the anterior column base, somewhat similar in size, shape, and coloration to the sepals and petals, ecalcarate; lamina fleshy, concave, deeply so toward the base, with two small basal lobes, recurved; callus consisting of a lobed basal ridge; nectar absent. *Column* lacking free filament and style, short; wings apparently forming a vestigial mitra, ruminate, shorter than the anther; column foot absent; anther terminal, four-celled, persistent, basifixed, suberect, bilobed; pollinarium present, consisting of four pollinia attached directly to a viscidium; pollinia clavate, granular, yellow; viscidium terminal; rostellum apical; stigma entire, basal, convex. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, glabrous, erect; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 33.2)

A monospecific genus endemic to New Caledonia. **(DJ)**

Fig. 33.2. Distribution map of *Coilochilus*.

Ecology

Coilochilus neocaledonicus grows between 500 and 1400 m in humid forests dominated by *Agathis* and *Araucaria* species and moist gullies in scrubby maquis developed on ultrabasic soils. **(DJ)**

Pollination

There have been no formal studies of the pollination of *Coilochilus*. Examination of flowers in the field by D. L. Jones (unpublished) indicated *C. neocaledonicus* is self-pollinating. This is supported by the illustration of a fruiting stem in Hallé (1977) showing that all flowers have set seed, a characteristic of autogamous species. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Can be difficult to maintain. It needs a basaltic soil mix and regular misting in active growth. **(DJ)**

Taxonomic literature

Hallé, N. (1977). *Flore de la Nouvelle Caledonie et Dépendances, 8. Orchidacées.* Muséum National D'Histoire Naturelle, Paris.

Schlechter, R. (1911). Die Polychondreae (Neottiinae Pfitz.) und ihre systematische Einteilung. *Botanisches Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*, **45**, 375–410.

34. CRYPTOSTYLIS

Cryptostylis R.Br., *Prodr.*, 317 (1810). Type species: *Cryptostylis erecta* R.Br.

Zosterostylis Blume, *Bijdr.*, **6**, t.1, f.32; **8**, 418 (1825). Type species: *Zosterostylis arachnites* Blume.

Chlorosa Blume, *Bijdr.*, **6**, t.1, f.31: **8**, 420 (1825). Type species: not designated.

Derivation of name

From the Greek *kryptos*, hidden, and *stylos*, pillar, column, referring to the short column of these orchids, which is partially hidden by the basal parts of the labellum. **(DJ)**

Description (Plates 36, 38; Fig. 34.1)

Perennial geophytic *herbs*. *Stems* short, subterranean, persistent, horizontal to vertical, producing new shoots at intervals from nodes; vertical shoots with membranous to scarious cataphylls at each node. *Roots* thick and fleshy, capable of producing shoots from damaged sites. *Tubers* absent. *Leaves* 1–few per shoot or absent, basal, petiolate; lamina mostly ovate-lanceolate, erect, coriaceous, convolute in bud, often abaxially with anthocyanin pigments, margins entire; venation anastomosing. *Inflorescence* racemose, few–

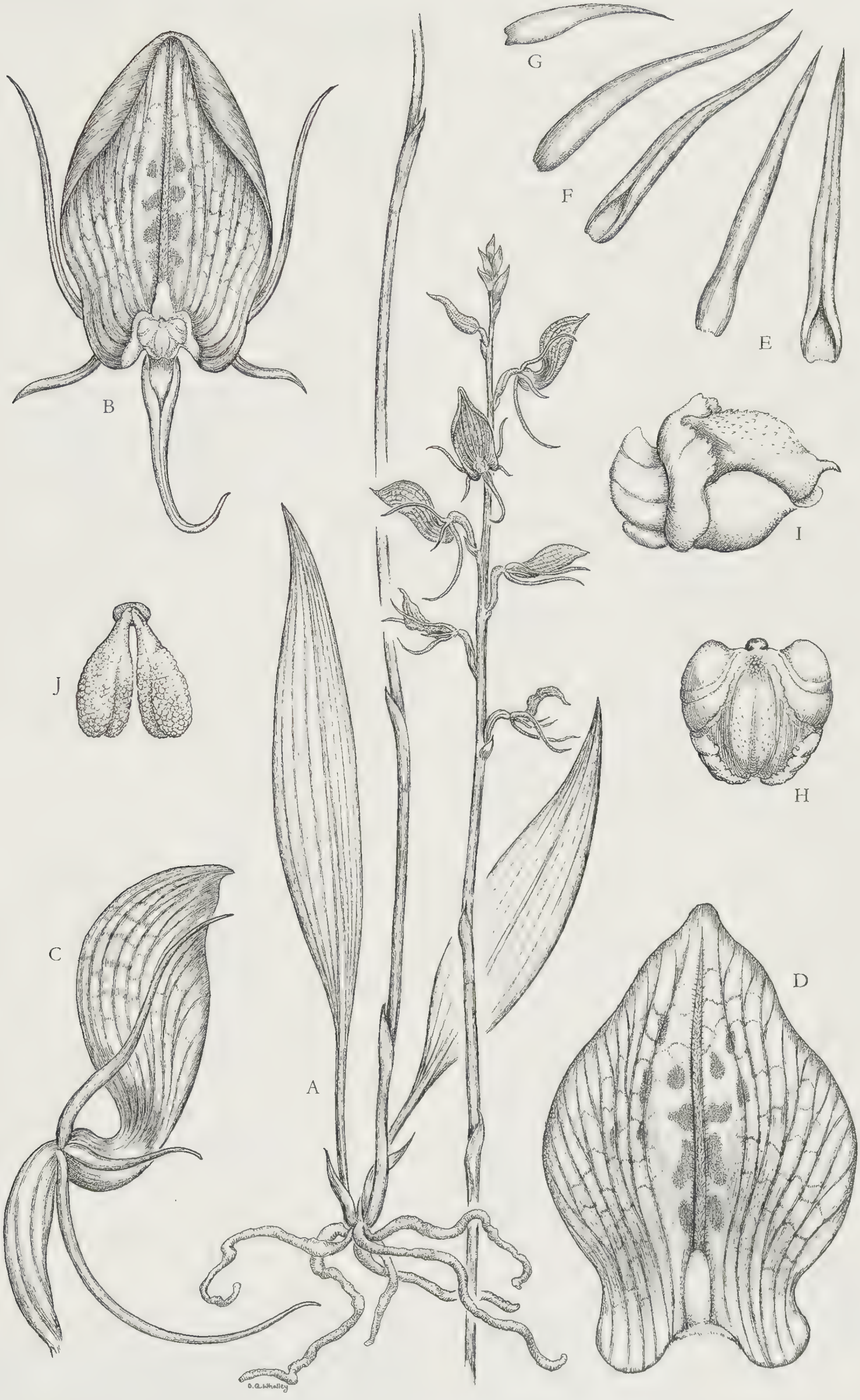

Fig. 34.1. *Cryptostylis erecta* R.Br. A. Habit, ×1.5; B. Flower from front, ×3; C. Flower from side, ×3; D. Labellum flattened out, from above, ×4.5; E. Dorsal sepal, front and back, ×3; F. Lateral sepal, front and back, ×3; G. Petal, ×3; H. Column from front, ×9; I. Column from side, ×9; J. Pollinarium, ×9. Drawn by Oliver Q. Whalley.

several flowered, erect, lateral; scape wiry to stout, with 2–6 sterile bracts; floral bracts foliaceous, sheathing. *Flowers* non-resupinate, dull-coloured, pedicellate. *Sepals* and *petals* much reduced and inconspicuous when compared with the labellum. Sepals free, similar, narrow. Petals free, smaller than the sepals. *Labellum* free, attached by its base to the anterior column base, conspicuous, markedly dissimilar in size, shape, and coloration to the sepals and petals, ecalcarate; lamina not lobed, porrect to recurved, basally expanded and closely embracing the column, covered with short glandular trichomes, the margins variously incurved or recurved; callus consisting of low longitudinal ridges or keels, often with associated dark, shiny, round to elongate, calli-like structures, sometimes with a terminal callus; nectar absent. *Column* lacking free filament and style, short; wings forming a vestigial mitra, appearing ragged, shorter or longer than the anther; column foot absent; anther terminal, four-celled, persistent, basifixed, erect, papillate, rostrate; pollinarium present, consisting of four pollinia attached directly to a viscidium; pollinia clavate, granular, yellow; viscidium terminal; rostellum ventral; stigma entire or lobed, convex. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, thin-walled, glabrous, erect; sepals and petals persistent; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 34.2)

A genus of about 25 species distributed in India, Sri Lanka, Taiwan, Thailand, Malaysia, Philippines, Java, Sumatra, Borneo, Solomon Islands, New Guinea, New Caledonia, Australia, New Zealand, Fiji, and Samoa. **(DJ)**

Phytochemistry

Several unusual tetrahydroisoquinoline alkaloids have been isolated from *C. fulva* Schltr. and *C. erythroglossa* Hayata (Fig. 34.3). The former species contains three substituted 1-phenyltetrahydroisoquinoline alkaloids known as (*S*)-cryptostyline I, II and III, all of which exhibit positive specific rotation values (Leander *et al.* 1969). An X-ray crystal structure determined for the methiodide of cryptostyline I confirmed the (*S*)-configuration for this compound proposed from earlier circular dichroism studies (Westin 1972; Brossi and Teitel 1971). All three compounds were found to have the same absolute configuration (Leander *et al.* 1973). *Cryptostylis erythroglossa* also contains these alkaloids but exclusively in the (*R*)-configuration (Agurell *et al.* 1974*a*). In addition, two related quaternary alkaloids were obtained as the salts, 6,7-dimethoxy-2-methyl-1-(3,4-methylenedioxyphenyl)isoquinolinium chloride and 6,7-dimethoxy-2-methyl-1-(3,4-methylenedioxyphenyl)-3,4-dihydroisoquinolinium iodide. (±)-Cryptostyline III has been synthesized in a three-step process from 3,4-dimethoxyphenylacetic acid and 3,4,5-trimethoxy-N-methylbenzamide, with an overall yield of 31% (Venkov *et al.* 1982). Some preliminary work on the biosynthesis of (*R*)-cryptostyline I has been presented (Agurell *et al.* 1974*b*). There have been no reports to date of the occurrence of any of the alkaloids described from *Cryptostylis* in other taxa. **(NV, RG)**

Ecology

With the exception of the Australian species *C. hunteriana* Nicholls, which is saprophytic, species of *Cryptostylis* are evergreen terrestrials that form small clumps. They can be readily identified, at least to genus, by their erect, prominently stalked leaves, which can be patterned or abaxially coloured. Plants tend to occur as isolated or scattered clumps but can be locally frequent in suitable environments. Most species seem to tolerate a wide range of edaphic and climatic conditions. *Cryptostylis subulata*, for example, is distributed from temperate to tropical regions and grows in sites with soils ranging from well drained to swampy. *Cryptostylis arachnites* Bl. occurs in a number of tropical countries and is found in humus-rich areas in rainforest, especially in mountainous districts. Even the saprophytic *C. hunteriana*, which might be expected to have rather specific requirements, is widely but disjunctly distributed from the subtropics to warm temperate regions. Flowering, even in the tropical species, seems to occur mainly in spring and summer. In the species from temperate regions the period from pollination to seed dispersal is 9–12 weeks but is much shorter in some of the tropical species. In *C. arachnites*, for example, it is not unusual for the lowermost capsules to be dehiscing while buds are still developing at the top of the inflorescence.

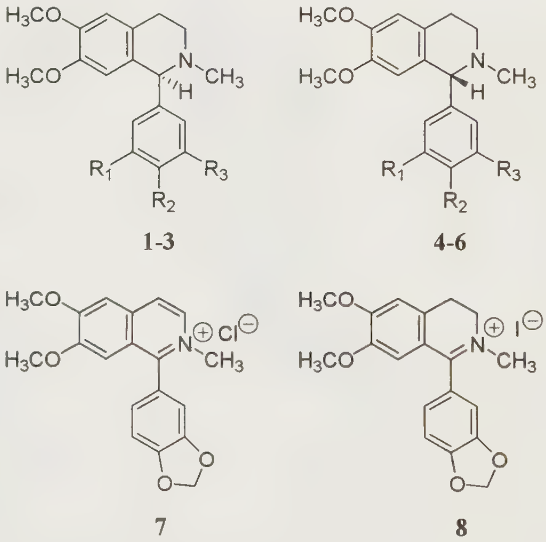

Fig. 34.3. Tetrahydroisoquinoline alkaloids of *Cryptostylis*.
(**1**) (*S*)-cryptostyline I, $R_1 = H$, $R_2 = R_3 = OCH_2O$; (**2**) (*S*)-cryptostyline II, $R_1 = H$, $R_2 = R_3 = OCH_3$; (**3**) (*S*)-cryptostyline III, $R_1 = R_2 = R_3 = OCH_3$; (**4**) (*R*)-cryptostyline I, $R_1 = H$, $R_2 = R_3 = OCH_2O$; (**5**) (*R*)-cryptostyline II, $R_1 = H$, $R_2 = R_3 = OCH_3$; (**6**) (*R*)-cryptostyline III, $R_1 = R_2 = R_3 = OCH_3$; (**7**) 6,7-Dimethoxy-2-methyl-1-(3,4-methylenedioxyphenyl)isoquinolinium chloride;
(**8**) 6,7-Dimethoxy-2-methyl-1-(3,4-methylenedioxyphenyl)-3,4-dihydroisoquinolinium iodide.

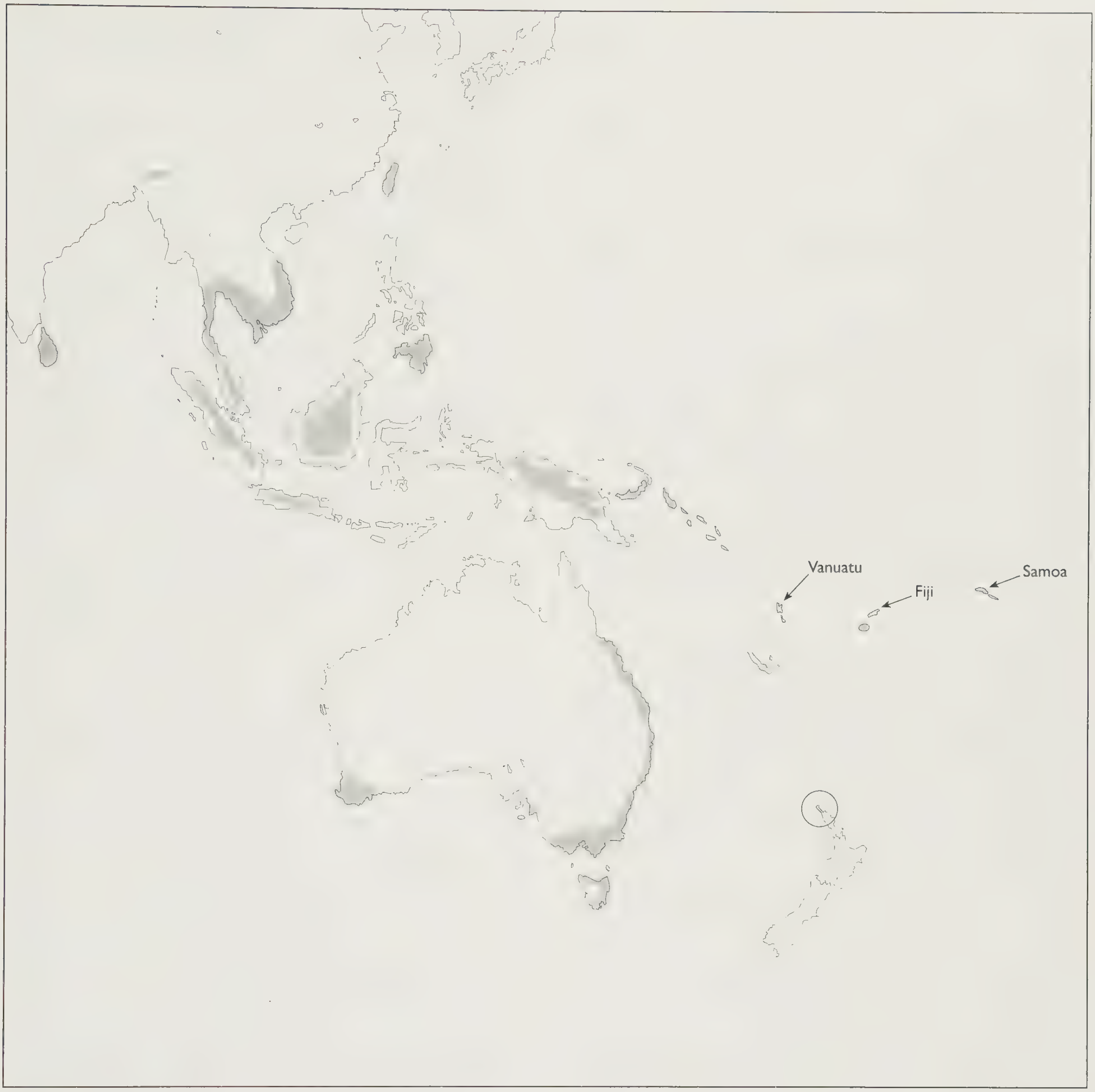

Fig. 34.2. Distribution map of *Cryptostylis.*

Cryptostylis has a wide latitudinal range extending from India and Taiwan (about 22° north) to southern Tasmania (about 43° south). Plants favour mesic situations in a variety of habitats. In the tropics they occur in moist forests, particularly rainforest, mostly at mid-elevations. In Borneo, for example, *C. acutata* J. J. Sm. ranges between 1100 and 2700 m, *C. arachnites* between 800 and 2200 m, and *C. clemensii* J. J. Sm. 1100 to 1700 m (Wood and Cribb 1994). The Australian and New Zealand species are usually found at low elevations and occur in moist to seasonally dry habitats such as sclerophyll forest and woodland, where they mainly grow in the soil but also are known to occupy clefts and crevices of large rocks and boulders. Other habitats include heathland, low-lying depressions among grasses and sedges, and swamps. **(DJ)**

Pollination

The remarkable pollination strategy of *Cryptostylis* was the first example of sexual deception or pseudocopulation detected in Australian orchids and is also the best known. In a brilliant and, at the time, controversial series of papers published between 1927 and

1938, Coleman revealed the essentials of pollination by pseudocopulation in *Cryptostylis.* Her daughter first drew her attention to the peculiar behaviour of the wasp, *Lissopimpla excelsa* (syn. *L. semipunctata*) (Ichneumonidae) on flowers of *C. leptochila* Benth. Instead of entering the flower head first, as is normal with nectar seeking insects, the wasp backed in and pressed its abdomen into a cavity at the base of the labellum. The pollinia were attached by the viscidium to the top of the abdomen near the tip and were removed with a jerk, indicating some resistance as the wasp withdrew. When in the flower, claspers at the end of the abdomen appeared to grip the base of the labellum.

Coleman's (1927) observations showed that the wasps were strongly attracted from a distance, indicating that a powerful scent was involved. Subsequently she realized that only males of *Lissopimpla excelsa* were drawn to the flowers and the flower itself bore an uncanny resemblance to the body of a female wasp. These observations gave rise to the theory (Coleman 1928*a*) that the flowers mimic the scent and appearance of the female and are pollinated when males attempt to mate with them. Coleman (1928*b*, 1929*b*, 1931*b*, 1938) made detailed observations of the behaviour of male *L. excelsa* to prove the sexual nature of the attraction by the orchids.

When inflorescences of *Cryptostylis leptochila* were exposed in localities where the orchids did not occur naturally, large numbers of male *Lissopimpla excelsa* could be attracted within a few moments of exposure. Competition for flowers was often fierce with several males attempting to enter simultaneously. Wasps approaching the flowers, particularly in the early part of the season (January), often exserted their aedeagus as if in readiness for mating (Coleman 1928*b*). After landing, the insects grasped the sides of the labellum near the centre with their front two pairs of legs, curved the abdomen into a sickle shape, and backed into the cavity at the base.

Claspers at the tip of the abdomen open and grasp a fleshy fold of labellum tissue into which the aedeagus is inserted (Coleman 1928*b*). When mating with females the abdomen is curved in the same fashion (Coleman 1928*a*, 1931*b*). If undisturbed, males may remain in the flower for several minutes performing rhythmical abdominal movements and ejecting seminal fluid. Wasps disengaged from flowers during pseudocopulation often had small droplets of liquid at the tip of the abdomen. When examined microscopically, spermatozoa were found in the liquid (Coleman 1928*b*). Ejaculation by *L. excelsa* in *Cryptostylis* flowers appears to be unique among sexually deceptive orchids. It does not occur in other well-studied systems, such as the thynnine-pollinated Caladeniinae and Drakaeinae in Australia or in *Ophrys* (Orchidinae) in Europe (Kullenberg 1961).

The wasps may be so intent on mating with the flower that they can be closely examined with a magnifying glass, even remaining attached to the flower if it is removed and placed in a jar. If a male is physically removed during pseudocopulation, resistance is felt due to the locking of the claspers onto the labellum. It seems clear from Coleman's (1928*b*, 1931*b*) observations that some form of sexual coupling with the base of the labellum takes place, indicating that structures mimicking the female genitalia may be present. This possibility has not been investigated.

Males disturbed before completing pseudocopulation will immediately return to the flower or seek another nearby. However, undisturbed males leave the flowers altogether after completing pseudocopulation. This ensures that most pollinia are transferred to other plants, perhaps some distance away (Coleman 1928*b*).

Observations on other *Cryptostylis* species (Coleman 1929*a*, 1930*a*, *b*, 1933*d*) showed that *C. subulata*, *C. erecta*, and the Western Australian *C. ovata* (Plate 37) were pollinated by *Lissopimpla excelsa* in a similar manner. To complete the picture, the rare *C. hunteriana* Nicholls is also pollinated by *L. excelsa* (Nicholls 1938), so that all five Australian species of *Cryptostylis* are pollinated exclusively by the same species of wasp. This seems extraordinary when the diversity of labellum shapes, position, and colouring in *Cryptostylis* is considered. The visual and tactile stimuli required by the male wasp must be quite generalized as it readily accepts the various labella and easily orients correctly for pseudocopulation. Nothing appears to be known about the pollinators of the remaining 15 or so *Cryptostylis* species in the Indomalaysian and Pacific regions, but it would not be surprising if all species in the genus are pollinated by *L. excelsa* (Coleman 1930*b*).

The narrow, erect, reddish labellum of *C. leptochila* has rows of shiny black calli and more obviously resembles the abdomen of the female than other species. The broad, erect, bonnet-shaped labellum of *C. erecta* has two central rows of irregular dark blotches, which may provide the necessary stimulus (Coleman 1930*b*). *Cryptostylis hunteriana* has a hairy, reddish labellum with a dark central line that breaks up into three rows of irregular spots toward the base. The labellum of *C. subulata* is bright red with two central black lines commencing near the base and terminating in a dark knob near the apex. In contrast to other species, the labellum hangs down in *C. subulata* so that the wasp must mate upside down, which it accomplishes with ease (Coleman 1929*a*).

Female *Lissopimpla excelsa* are reddish with a black abdomen marked with two rows of irregular white spots. The broken black lines of all *Cryptostylis* species, except most *C. subulata*, apparently mimic the spotted black abdomen of the female. The red colour of the female's thorax and legs probably also contributes to the stimulus. The bright red of *C. subulata* may compensate for the unbroken black central lines in this species, and the knob-like process may mimic the female wasp's head, thereby assisting the male in orientation.

Coleman (1929*b*) noted that *Lissopimpla excelsa* males alight on *Cryptostylis subulata* with the head on or near the knob and then back into the flower. Graham (1983) observed that 35 out of 40 wasps visiting *C. subulata* in New Zealand landed on the flower in the correct position to back into the column, indicating that the orientation of the pseudofemale is usually perceived as the insect approaches. Those landing in other positions quickly assume the correct posture. By contrast to other species, *C. erecta* is more brownish purple than red, and the central pattern is also brownish purple rather than black.

Lissopimpla excelsa males were active on warm to hot, sunny days with a light breeze (Coleman 1927; Graham 1983). Most activity occurred between 8:30 and noon, though some wasps responded as late as 16:10 in New Zealand. The majority approached from downwind of the orchids (Graham 1983) as if following an odour trail. The most important stimulus appears to be the initial olfactory cue, which triggers the subsequent behaviour.

There have been several anecdotal demonstrations of the powerful, long-distance olfactory attraction by *Cryptostylis* flowers for male *L. excelsa*. Wasps are often attracted through open windows of houses or vents in glasshouses to orchids that are effectively invisible from outside (Coleman 1928*a*; Whitehead 1964; Clemesha 1964; Wallace 1978). *Lissopimpla excelsa* is abundant and widespread, with a distribution much greater than that of *Cryptostylis* in south-eastern Australia. Orchids in glasshouses as far as 100 km from the nearest known or ecologically likely occurrences of *Cryptostylis* may attract *L. excelsa* males (Whitehead 1964; Wallace 1978). Coleman (1930*b*) observed that flowers of *C. erecta* covered in muslin attracted wasps; similar results were obtained by Graham (1983) for *C. subulata*.

Two extraordinary observations indicated that *Cryptostylis* flowers are more attractive to male individuals of *L. excelsa* than their own females. Coleman (1931*b*) placed a female *L. excelsa* in a glass jar covered in butter muslin through which any pheromone could readily disperse. The jar and some flowers of *C. subulata* and *C. leptochila* were exposed in the open. Almost immediately six to eight male wasps visited the orchids, but none paid any attention to the jar with the female. Many more males were attracted to the flowers over the next 20 minutes, all ignoring the female. Eight males were then placed in the jar with the female. One or two attempted to mate with her, adopting the same posture as they did with the flowers. Two flowers of *C. leptochila* were then introduced to the jar. The males rushed to them, attempting to enter two at a time, apparently preferring the flowers to the female. This observation needs to be treated with some caution as it involved only a single female that may not have been receptive at the time (Coleman 1931*b*), and therefore not emitting pheromone. Nevertheless, it does appear that the flowers, in combination with the pseudopheromone emission, were visually more stimulating than the female.

An even more extraordinary event, demonstrating the preference by a male for *C. ovata* flowers over a female, was witnessed by Coate (1965). While carrying an inflorescence of *C. ovata* she observed a male wasp, in copula with female, flying toward the flowers. Suddenly the male discarded the female in mid-air before landing on the labellum and backing into it. The rejected female sat nearby before flying off. These observations indicate that the olfactory and visual stimuli offered by *Cryptostylis* species are much greater than those of females. Such stimuli may be termed 'supernormal' (Tinbergen 1964). The orchid flowers are much larger than the female and apparently exaggerate the features sought by the male, thereby presenting him with a highly attractive stimulus.

Coleman (1928*a*, *b*; 1931*b*) noted that male wasps seemed more numerous and eager at the start of the season. She suggested males might emerge earlier than females and may be more likely to respond to orchids before females are present. This postulate was stated as if it were fact by Wallace (1978), but there is no direct evidence to support the idea, even though it may seem advantageous that males be available as soon as females appear. Certainly in some wasps males may emerge a short time before females (Burrell 1935; Given 1957), but the difference is unlikely to be more than a few days or a week, as there is no advantage in males emerging too soon. The impressions of early male emergence, and sex ratios biased strongly in favour of males, may simply be attributable to their greater conspicuousness as a result of the strong attraction to the orchids. Coleman (1931*b*) provided some evidence of a biased sex ratio when seven males emerged from a batch of parasitized sawfly pupae. However, this observation simply reflects the arrhenotokous reproductive system of most hymenoptera in which unmated females produce haploid males by parthenogenesis (Naumann 1991).

Coleman (1928*b*) noted that visits by male *L. excelsa* to *Cryptostylis* flowers declined later in the season, and of those landing on the flowers, few exserted the aedeagus or attempted copulation. However, in one year, males responded vigorously to *C. subulata* as late as mid-March, entering flowers two or three at a time (Coleman 1933*d*). Coate (1965) observed that *L. excelsa* males were strongly attracted to *C. ovata* throughout the flowering period, except on dark cold days. Thus the available observations are contradictory and preclude definite conclusions. Several explanations are possible for declining responses by wasps to orchids during the season. These include learning by wasps to avoid flowers, loss of vigour with age, and natural mortality. Careful experimentation is required to measure any declines in response and isolate the causes.

If, as Coleman (1928*a*,*b*; 1931*b*) suggested, males are more active on *Cryptostylis* flowers early in the flowering period, it would be expected that a higher proportion of early flowers would be fertilized than later ones. The limited data available support this. Coleman (1928*a*) noted that of the few flowers pollinated in most populations of *C. leptochila* (less than 7% in one sample) it is usually the earliest flowers that develop seed capsules. Data presented by Graham (1983) support Coleman's hypothesis. He found that only six flowers were pollinated out of 73 on five plants, and all were near the base of the raceme. It may be that *L. excelsa* learns to avoid *Cryptostylis* plants, so that later flowers have less chance of being pollinated. This raises the question of why flowering is not concentrated early in the season rather than being spread over a relatively long period of 8 to 12 weeks or more.

Stoutamire (1975) observed that although a wasp may visit several flowers it picks up only one pollinarium. The first pollinarium appeared to prevent attachment of a second viscidium, indicating that the positioning of the pseudocopulating male is stereotyped. However, this result is contradicted by Coleman (1928*a*, *b*, 1931*b*) and Graham (1983) who reported that two or three pollinaria may frequently be carried by a single wasp. In one case a small male was captured with seven pollinaria on the last three segments of its abdomen (Coleman 1933*d*).

When pollinia are removed from the anthers, they are held initially at right angles to the wasp's body (Coleman 1928*a*). Later they assume a parallel position, which Coleman (1928*a*) considered was due to backward depression of caudicles as the viscidium dries. However, *Cryptostylis* species lack caudicles (Dressler 1981, 1993; illustrations in Nicholls 1969, Fig. 34.1), the pollinia being attached directly by their narrow apices to a viscidium. Depression of the pollinia, probably simply under their weight, brings the pollinia into the correct position to contact the stigma of another flower. Only a portion of the pollen massulae are transferred to the stigma at each visit so that one pollinarium may fertilize several flowers (Stoutamire (1975).

The four species of *Cryptostylis* found in south-eastern Australia overlap considerably in distribution; populations of two or even three species may flower simultaneously in close proximity to each other. As they share the same pollinator, pollen transfer between species seems highly probable. Despite this no hybrids have been recorded in *Cryptostylis* (Stoutamire 1975). Coleman (1929*b*) showed that the same wasp will visit flowers of *C. subulata* and *C. leptochila* indiscriminately. Similar observations were made by Stoutamire (1975), who set up flowers of *C. subulata*, *C. erecta*, and *C. leptochila* in bushland to observe the behaviour of visiting *L. excelsa*. A preference was often shown by visiting males for one flower or another, but several individuals subsequently visited a second species. Stoutamire (1975) suggested the preference may have been due to differences in pheromone production, possibly influenced by the age of the flower or some other factor.

Experimental crosses within and between *Cryptostylis* species (Stoutamire 1975; Jones 1988) show that there are physiological or genetic barriers to hybrid formation. Mature embryos only resulted from crosses between different plants of the same species (Stoutamire 1975). Self-pollination and crosses between species failed. By contrast, Johns and Molloy (1983) reported that self-pollination of *C. subulata* in New Zealand resulted in ample seed set. Coleman (1928*a*, *b*) suggested that self-pollination occurred infrequently in *Cryptostylis*. She observed that wasps usually remove pollinia cleanly and without difficulty, but occasionally a wasp would twist around to free its claws, which embed in the labellum. This action may result in pollen, that has just been removed from the anther being smeared on the stigma (Coleman 1928*a*). Coleman (1929) and Graham (1983) noted that self-pollination may also occur when wasps revisit the same flower. The latter noted that on two occasions, when only a single fresh flower was available, wasps that had earlier removed the pollinia returned after about an hour and re-entered the flower. In other cases, highly motivated wasps re-entered the same flower on the first visit repeating pseudocopulation up to 19 times before leaving (Graham 1983).

Although a great deal has been learned about the fascinating reproductive strategies of *Cryptostylis*, there are many contradictory statements in the literature supported by few hard facts. Detailed studies are still needed to determine the degree of outcrossing versus selfing and understand the life cycle and behaviour of *L. excelsa* in relation to the flowering period and pollination of *Cryptostylis* species. **(CCB)**

Uses

The only use documented for *Cryptostylis* is as ornamentals by specialist growers. **(DJ)**

Cultivation

This genus differs from most other Diurideae in that the plants grow from a rhizome and tuberous roots, and the leaves have a life of several years. New leaves are produced annually after flowering time. Four of the five Australian species have been successfully cultivated—*C. erecta* R.Br., *C. leptochila* Benth, *C. subulata*, and *C. ovata* R.Br.—but they require special conditions and patience as they can be slow to grow.

Cryptostylis species have thick rhizomes and are slow to re-establish after disturbance, so it is best to grow them in a larger pot to allow plenty of room for rhizome growth. Repot only when necessary. Broken pieces of rhizomes can be potted up to grow on from dormant buds, although several years may elapse before they sprout.

Mix: basic with extra drainage material. Sphagnum moss has also been used successfully. Light: 50% shade. Watering: as these are evergreen, they need to be kept damp all the time. Some growers stand the pots in a saucer to retain water. Flowering: Australian species flower over summer so must not be allowed to dry out over that time, in contrast to other Diurideae. Propagation: the rhizomes multiply, so when the pots become overcrowded the plants need to be divided, taking care not to break the brittle rhizomes. They can also be propagated from seed scattered around parent plants. **(HR)**

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SUBTRIBE DIURIDINAE

Diuridinae Lindl., *Gen. Sp. Orch. Pl.*, 442, 506 (1840). Type: *Diuris* J. J. Sm.

Description

Glabrous, tuberous, geophytic *herbs. Tubers* elongate, naked. *Leaf* 1–several, convolute, sessile, much longer than wide, erect, channelled. *Inflorescence* racemose. *Flowers* resupinate, dull or brightly coloured; tepals markedly dissimilar; petals reduced or clawed. *Labellum* fixed to the base of the column; lamina three-lobed, without calli. *Column* with stamen and style almost free; column foot absent; pollinarium present; pollinia four. *Fruit* a dehiscent capsule. **(DJ)**

Anatomy

Leaf

SURFACE

Hairs absent, except papillae in *Diuris sulphurea* R.Br. abaxially at midrib and margins. Epidermis: cells rectangular, trapezoidal, rhomboidal, axially elongated; walls mostly thin without conspicuous pit-fields, somewhat sinuous in *D. semilunulata* Messmer. Stomata on both surfaces.

TRANSECTION

Cuticle thin, variable in sculpturing. Epidermis: cells isodiametric, elliptical to ovate, often anticlinally elliptical or S-shaped; outer wall thickened. Stomata superficial (slightly elevated in *D. longifolia* R.Br.), substomatal chambers shallow, except connected to long, transverse lacunae in mesophyll of *D. lanceolata* Lindl. Mesophyll homogeneous or heterogeneous, depending on species. Palisade mesophyll 1–2 layers, abaxial or bifacial. Transverse lacunae present in some species. Vascular bundles as for the tribe. Crystals: raphides and rod-shaped crystals common in mesophyll idioblasts.

Stem

TRANSECTION

Hairs absent. Cuticle thin, smooth to rugose in *Diuris*, striate in other genera. Epidermis: cells isodiametric, rectangular, elliptical to polygonal; outer wall thickened in all species except *D. sulphurea*, inner wall also thickened in *Orthoceras*. Stomata present, superficial in *D. aurea* J.J.Sm., *D. semilunulata*, and *Orthoceras*. Ground tissue parenchymatous, innermost layers sclerotic, forming a sclerenchyma sheath. Vascular bundles as for the tribe, in 1–4 rings, the outer ring abutting sclerenchyma sheath if present. Xylem tracheids mostly with helical and scalariform thickenings. Crystals: raphides or rod-shaped crystals in cortex and/or pith of many species.

Tuber

TRANSECTION

Hairs absent. Velamen 1–3 layered, cells elliptical to polygonal, often periclinally compressed; walls of uniform thickness or outer wall thicker. Exodermis: cells elliptical to polygonal, walls of uniform thickness or outer wall thicker. Cortex parenchymatous, outer layers often dissociated, infrequently infected with hyphae and pelotons. Endodermis: cells elliptical to polygonal. Stele medullated, 5–34 arch depending on species. Xylem tracheids with helical, scalariform or pitted thickenings. Ergastic substances: starch grains and raphides or rod-shaped crystals in cortex of some species.

Root

TRANSECTION

Hairs absent. Velamen 1–2 layered, cells elliptical to irregularly polygonal, often periclinally compressed; walls of uniform thickness or outer and/or radial walls of outermost layer thicker depending on species. Unicellular organisms present in some velamen cells. Exodermis: cells elliptical to polygonal, walls of uniform thickness (except outer wall thicker in *D. longifolia*, *D. magnifica* D. L. Jones, and *D. picta* J. L. Drumm.). Cortex parenchymatous, outer and/or middle layers often infected with hyphae and/or pelotons. Endodermis: cells elliptical to polygonal. Stele medullated, 4–9 arch. Xylem tracheids with helical, scalariform or pitted thickenings. Crystals: raphides or rod-shaped crystals in cortex. **(AP)**

Key to the genera of Diuridinae (DJ)

1. • Flowers brightly coloured; petals large, with a prominent lamina and a basal claw; lateral sepals channelled, descending below the labellum; column wings not papillate . . . .**35. *Diuris***
   • Flowers dull-coloured; petals tiny, sessile; lateral sepals filiform-terete, spreading or erect beside the dorsal sepal; column wings papillate . . . . .36. *Orthoceras*

Phytochemistry

There are no phytochemical data recorded for Diuridinae. **(NV, RG)**

Phylogenetics

This taxon has consistently been recognized as distinct (as a division or subtribe) within Neottieae (= subfamily Orchidoideae) from its inception. The winged staminodia separated from the remainder of the column characterize the subtribe. In most other respects *Diuris* and *Orthoceras* are, however, similar to many taxa in Diurideae. Accordingly these taxa have historically been linked to the remainder of the Diurideae, especially those taxa possessing root tubers, such as found in Thelymitrinae, Acianthinae, and Caladeniinae. This proposition has been confirmed through embryological studies (Clements 1995) and DNA sequence analysis (Kores *et al.* 1997, 2000). **(MAC)**

35. DIURIS

Diuris J.J.Sm., *Trans. Linn. Soc. London*, **4**, 222 (1798). Type species: *Diuris aurea* J.J.Sm.

Derivation of name

From the Greek *dis*, double, and *oura*, tail, referring to the conspicuous, lateral sepals that project below the labellum. **(DJ)**

Description (Plates 39, 40; Fig. 35.1)

Perennial geophytic *herbs*. *Roots* filamentous. *Tubers* ovoid or cylindrical, paired, fleshy, naked; replacement tubers produced on the end of short droppers; daughter tubers absent or formed on the end of short to long, slender root-like stolons or sometimes on extra short droppers. *Stem* erect, short, unbranched, terete, with membranous cataphylls at each node. *Leaves* basal, 1–several per shoot, distichous or spirally arranged, sessile; lamina much longer than wide, erect to lax, convolute in bud, conduplicate, margins entire; venation anastomosing. *Inflorescence* racemose, 1–many flowered, erect, terminal; scape wiry, with 1–3 sterile bracts, the lowest bract often extended and leaf-like; floral bracts foliaceous, sheathing. *Flowers* resupinate, brightly coloured, pedicellate. *Dorsal sepal* free, shorter and broader than the lateral sepals, cucullate proximally over the column, distally erect or reflexed. *Lateral sepals* free, longer and narrower than the dorsal sepal, descending as paired tails below the labellum. *Petals* free, dissimilar to the sepals, consisting of a basal claw and terminal expanded lamina. *Labellum* free, attached by its base to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina strongly three lobed, the lateral lobes closely flanking the column, often widely spreading distally, the mid-lobe keeled or folded longitudinally with spreading margins, distal margins entire, crenate or undulate; callus of one or two proximal longitudinal ridges or keels, smooth or densely papillate, sometimes breaking up into narrow accessory ridges; nectar absent. *Column* with stamen and style nearly free, short; wings narrow, fused only at the base, erect and flanking the filament and style; column foot absent; anther dorsal, erect, parallel to the axis of the filament, two-celled, persistent, basifixed; pollinarium present, consisting of two pollinia attached directly to a viscidium; pollinia clavate, mealy, white; viscidium dorsal; rostellum apical; stigma entire, large, scutiform. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, thin-walled, glabrous, erect; pedicels not elongating in fruit. *Seeds* numerous, light to dark coloured, winged. **(DJ)**

Distribution (Fig. 35.2)

A genus of about 55 species distributed mainly in Australia with one species endemic to Timor. **(DJ)**

Palynology

Tetrads of *Diuris maculata* J.J.Sm. are globose-spherical, *c.* 36 μm, decussate; inaperturate; semitectate; and reticulate (Ackerman and Williams 1981). **(AP)**

Ecology

Diuris has a wide latitudinal distribution extending from 9° 30′–9° 50′ south in Timor to about 43° south in Tasmania. All species are terrestrial, and most grow as individuals or sparse colonies. Vegetative reproduction is prominent in some species, particularly members of the *D. longifolia*/*D. corymbosa* Lindl. group, which form localized clonal colonies. Some species such as *D. palustris* Lindl. can develop more than one new tuber annually and form localized tufts. All species, including those growing in the tropics, occur in areas with a seasonal climate, and the plants have periods of active growth and dormancy. When dormant the plants survive extremes of heat, low humidity, and dryness as fleshy tubers. The leaves of all species are fully expanded prior to flowering.

In Australia the greatest diversity within the genus occurs in the south-east and the south-west. The majority of species are found from the lowlands to about 800 m, but *D. monticola* D. L. Jones grows from montane to subalpine zones up to about 1800 m. Here it occupies tussock grassland and herbfield. Other species occur in a range of mesic habitats that at least in eastern Australia are strongly centred around grasslands and also sclerophyll forests and woodland, particularly those with a shrubby or grassy ground layer. Other habitats include *Callitris* woodland, mallee shrubland, granite outcrops, stabilized coastal dunes, coastal headlands, and heathland. Most species grow in well-drained soils, but a few species from Western Australia are restricted to winter-wet swamps, often growing with the base of the plants and leaves submerged.

Diuris species flower mostly in spring, between September and November, with a few species such as *D. heberlei* D. L. Jones and *D. monticola* flowering over summer. Two western species, *D. brumalis* D. L. Jones and *D. recurva* D. L. Jones, flower in winter. *Diuris oporina* D. L. Jones, from tropical north-eastern Queensland, is

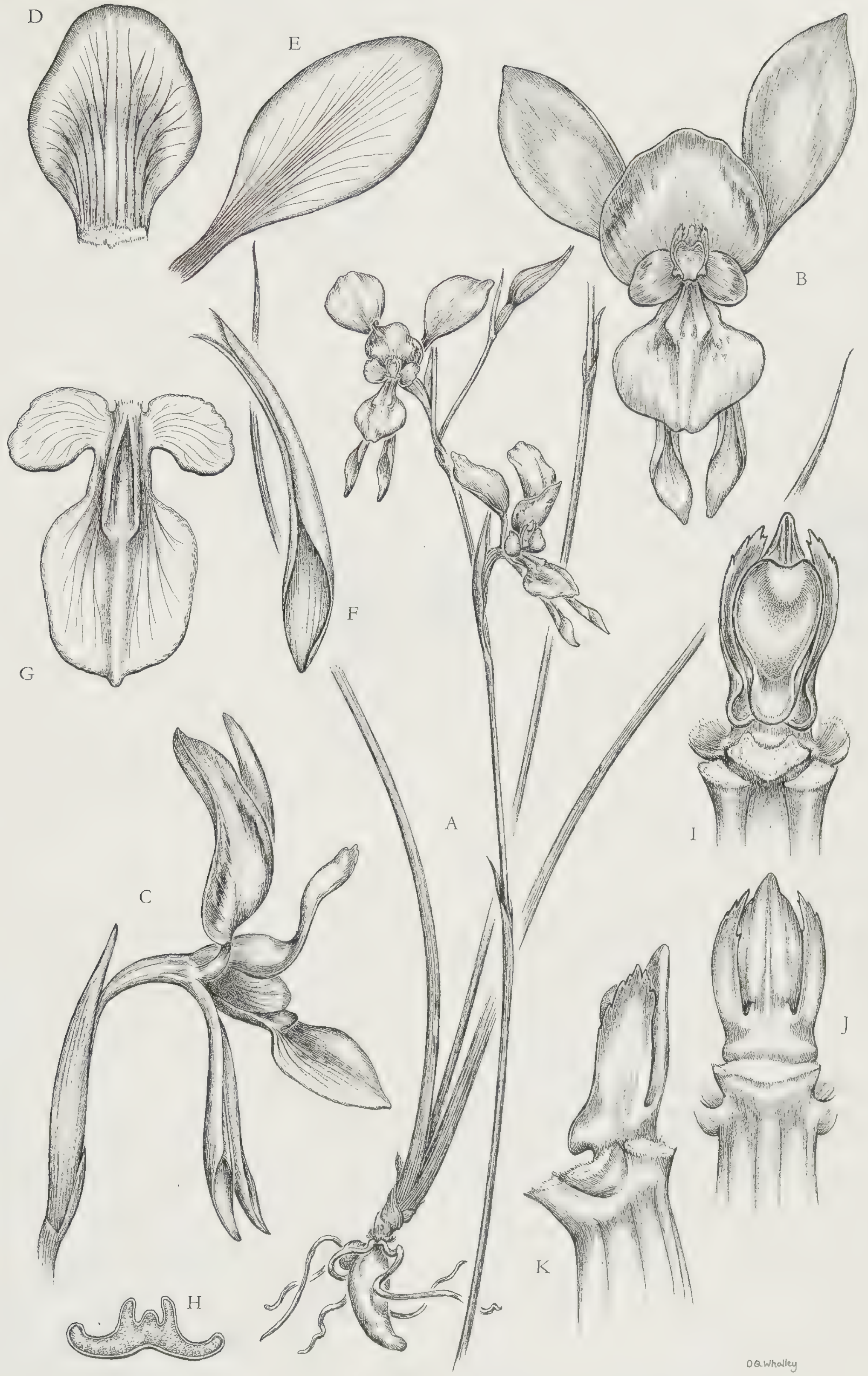

Fig. 35.1. *Diuris aurea* J.J.Sm. A. Habit, ×0.9; B. Flower from front, ×2.7; C. Flower from side, ×2.7; D. Dorsal sepal, ×2.7; E. Petal, ×2.7; F. Lateral sepal, ×2.7; G. Labellum, ×2.7; H. Labellum base, transverse section, ×8.1; I. Column from front, ×5.4; J. Column from behind, ×5.4; K. Column from side, ×5.4. Drawn by Oliver Q. Whalley from Kew Spirit Collection no. 18559.

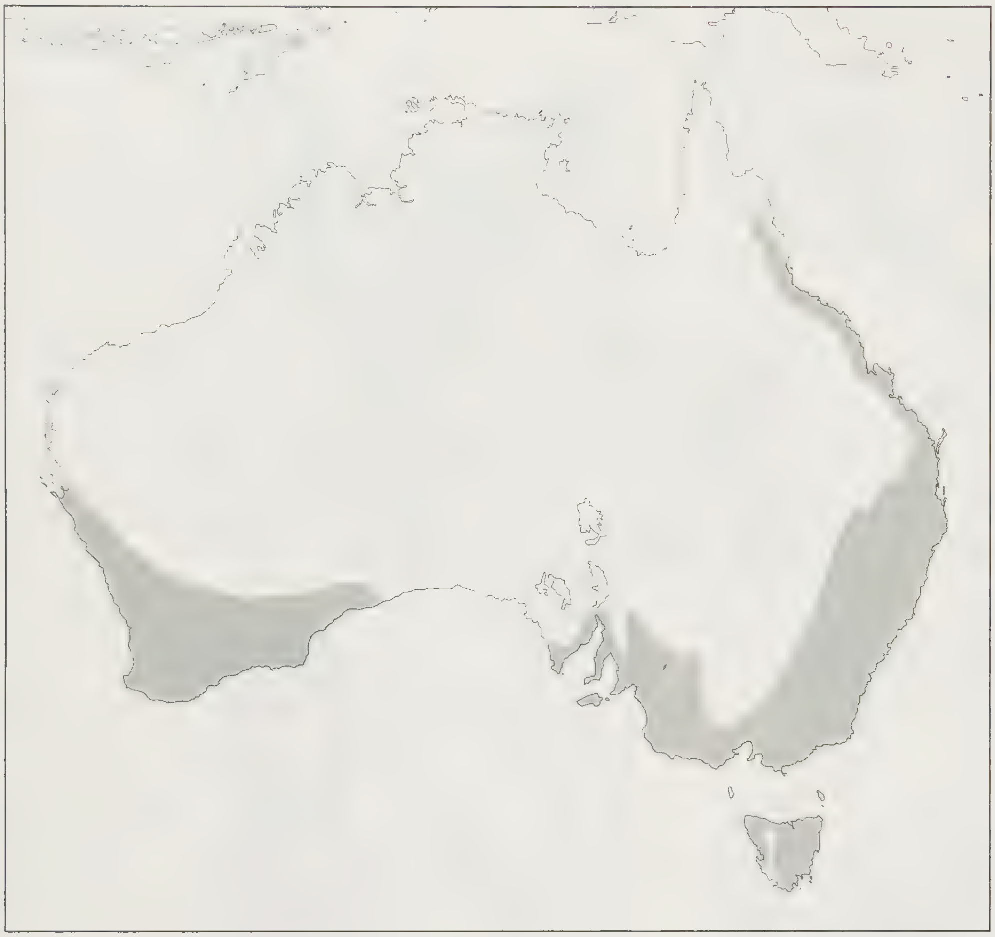

Fig. 35.2. Distribution map of *Diuris.*

unusual for its autumnal flowering. As a general rule, species from open habitats flower regularly in the absence of fire, but as the vegetation increases in density flowering may be reduced, and summer burns may have a promoting effect. In a number of species, including members of the *D. longifolia/D. corymbosa* group and many of the swamp-dwellers from Western Australia, summer fires have a dramatic effect on flowering and result in massed floral displays. *Diuris purdiei* Diels is totally fire-dependent and needs the stimulus of a summer burn before it will flower. Dispersal of seed begins 8–12 weeks after pollination.

In Timor, *D. fryana* Ridl. grows on grassy ridges and slopes. **(DJ)**

Pollination

Diuris flowers are brightly coloured in shades of yellow, orange, white, and purple, often with darker markings. These colours are typical of species pollinated by food-seeking insects such as bees, wasps, and flies. However, no *Diuris* species is known to produce nectar (Coleman 1932; Beardsell *et al.* 1986). Most species do not produce a detectable odour, although *D. punctata* J.J.Sm. is fragrant, *D. palustris* Lindl. has a spicy perfume in warm weather (Jones 1988), and *D. behrii* Schltdl. (as *D. pedunculata* R.Br.) has a 'slight perfume' (Coleman 1932) or a 'strong sweet fragrant perfume' on a warm day (Nash 1979). These characteristics indicate that *Diuris* species falsely advertise the presence of food and are pollinated by deceived insects seeking nectar or pollen. However, clear evidence supporting this hypothesis is available for only one species, *D. pardina* Lindl. (as *D. maculata* J.E.Sm.; Beardsell *et al.* 1986). Less-convincing data show that two other species, *D. behrii* (as *D. pedunculata*) and *D. sulphurea* R.Br., may be pollinated by sexually deceived male bees (Coleman 1933*c*; Bates 1977).

The *Diuris* column is a remarkably short structure, such that the heart-shaped stigma is situated at the base of the labellum. The two-celled anther is located directly behind the stigma, each cell containing a bilobed pollinium. The apices of the pollinia are attached directly to a prominent viscidium slotted into the rostellum in the central upper margin of the stigma. Two column wings flanking each side of the stigma also arise separately and have been interpreted as staminodes (Rogers 1921). There is debate as to whether this arrangement in *Diuris* represents the ancestral condition or is a secondary consequence of column shortening (Dressler 1993). Ontogenetic studies of column development are needed to confirm the staminodial hypothesis.

The position of the stigma means that insects probing for nectar at the labellum base or pressing their heads against the column will contact the viscidium and remove the pollinarium on the front of the head. Because of the location of the anther behind the stigma, the pollinia hang in the correct position on the pollinator's face to contact the stigma of the next flower visited. The location of the anther behind the stigma also makes autogamy mechanically impossible (Coleman 1932; Beardsell *et al.* 1986), and no cases of autogamy have been reported in *Diuris*.

Apart from one nectar-feeding wasp, *Gasteruption* sp. (Beardsell *et al.* 1986), all insects recorded removing pollinaria from *Diuris* species have been bees (Apoidea). Rayment (1932) reported the removal of pollinia on the frons by a species of *Paracolletes* (Colletidae), but the *Diuris* species involved is unclear. Coleman (1932, 1933*b*) found that *D. pedunculata* R.Br. var. *gigantea* Nicholls (= *D. behrii* Schldl.) in Victoria was visited and pollinated only by the bee, *Halictus languinosus* (= *Lasioglossum lanarium*; Halictidae). Coleman (1933*c*) observed that *D. sulphurea* was pollinated by reddish brown bees with yellow abdominal bands, but she was unable to capture it. Nash (1979) found in South Australia that *D. pedunculata* (probably *D. behrii*) was also pollinated by *Lasioglossum lanarium* (Halictidae). Beardsell *et al.* (1986) collected bees bearing the pollinia of *D. maculata* (actually *D. pardina*) as they foraged on flowers of *Daviesia* spp. (Fabaceae). Three specimens belonged to an undetermined species of *Leioproctus* (Colletidae), six belonged to two species of *Trichocolletes* (Colletidae), and one was the introduced *Apis mellifera* (Apidae). One specimen of *Leioproctus* with pollinia was captured as it visited a *D. pardina* flower.

In all cases pollinaria were collected on the face of the pollinator. In smaller bees the viscidium attaches to the frons between the antennae, whereas on larger bees it tends to be deposited lower down on the clypeus or labrum. The uniform placement of pollinaria provides the opportunity for hybridization if bees visit more than one *Diuris* species. Since hybrids are relatively frequent in *Diuris* (Jones 1970*a*,*c*, 1988; Ulherr 1970*a*; Beardsell 1975; Bates 1978*a*, 1986*a*), it is evident that a degree of interspecific pollen transfer can occur.

It is not uncommon for bees to collect multiple pollinaria from visits to several flowers. Coleman (1932) observed an individual of *Lasioglossum lanarium* enter three *D. behrii* flowers in succession and remove three pollinaria, forming a large, pale yellow mass on the forehead. She found up to five viscidia on the frons of captured specimens. Nash (1979) observed an individual *L. lanarium* collect two *D. behrii* pollinaria in captivity. Of the bees collected by Beardsell *et al.* (1986) with pollinaria of *D. pardina*, seven carried a single pollinarium, three bore two, and one had three. Bees frequently attempt to remove pollinaria from their faces and may leave them on the floral segments of the orchid or on nearby plants (Coleman 1932; Nash 1979).

The mechanism of attraction of bees to *Diuris* flowers has been clearly established for only one species, *D. pardina* (as *D. maculata*), at a site in southern Victoria (Beardsell *et al.* 1986). *Diuris pardina* is a floral mimic of the nectar-and-pollen-rewarding shrubs in the genera *Daviesia*, *Pultenaea*, and relatives (Fabaceae), which have masses of brightly coloured yellow or orange flowers with red or maroon markings. *Diuris pardina* and related species have flowers of similar shape and colour but about twice the size. Colletid bees of the genera *Leioproctus* and *Trichocolletes*, which bore pollinaria of *D. pardina*, also carried mainly legume pollen, primarily from *Daviesia* and *Pultenaea*, which have similar flowering times as *D. pardina*. Both male and female bees had picked up pollinaria of *D. pardina*, indicating the mechanism was not sexual attraction.

The upright standard petal of the pea flower is mimicked by the dorsal sepal and labellum lateral lobes of *Diuris*, and the horizontal *Diuris* labellum is equivalent to the wing petals. Bees landing on the wing petals probe between them to gather the copious nectar at the base of the corolla and pollen from the stamens. Leverage to push the wing petals apart is gained by pressing the head against the standard petal. A similar action by bees visiting *D. pardina* results in the head being pushed against the stigma and rostellum with ensuing pollination if the bee is carrying pollinia and removal of the pollinarium if one is still present.

Several workers (Coleman 1932; Rupp 1948; Bates 1977, 1986*a*) have suggested that the prominent callus ridges at the base of the labellum of many *Diuris* species function both as footholds to provide leverage and as guiding lines or a guiding channel to direct the bee to the base of the labellum. The mimicry of Leguminosae (Papilionoideae) may indicate a different role for the ridges (C. C. Bower, unpublished). The channel between the ridges may substitute for the gap between the wing petals through which the bees normally probe. In unsuccessfully attempting to push through the labellum channel, bees would press hard against the column to gain leverage, thereby effecting pollination.

Beardsell *et al.* (1986) found that *Diuris pardina* flowers were much less common than the species it was mimicking, about one in 10 000. Over the flowering period the pollinaria were removed from 63% of *D. pardina* flowers, but only 19% were pollinated. They concluded that the low frequency of pollination was attributable to poor pollinator fidelity and the low frequency of orchid flowers relative to pea flowers. Poor pollinator fidelity may result from an ability of bees to learn to avoid non-rewarding flowers. Some bees were observed by them to approach *D. pardina* flowers but then shun them. Those that did land withdrew quickly by contrast to the prolonged foraging visits on pea flowers. The much larger flowers of *D. pardina* than the pea flower models may serve as an exaggerated mimic or supernormal stimulus to provide enhanced attraction, possibly to help counteract learned avoidance reactions. The extreme variability in many *Diuris* species (Jones 1970*c*, 1988, 1991, 1998*d*; Bishop 1996) may also increase the time and number of encounters it takes for bees to learn avoidance. The low frequency of the mimic relative to the model is also important for minimizing learned avoidance and is a well-known characteristic of Batesian mimicry.

The possibility of sexual deception of male bees as a pollination mechanism in *Diuris sulphurea* and *Diuris behrii* (as *D. pedunculata*) has been raised by Coleman (1933*c*) and Bates (1977), respectively. In addition, others have interpreted Coleman's work on *D. behrii* as indicating sexual deception (Beardsell *et al.* 1986). By contrast still others have interpreted Coleman's (1932, 1933*c*) results as simply exemplifying floral mimicry (Dafni and Bernhardt 1990).

According to Coleman (1932) a Victorian population of *D. behrii* was pollinated exclusively by males of a single bee species, *L. lanarium.* Some 21 collected specimens were all males. Similarly, Bates (1977) trapped 45 specimens of a *Lasioglossum* species attracted to *D. behrii* in South Australia; all were males. Nash (1979) captured two male *L. lanarium* on *D. behrii*, also in South Australia. The lack of females in these collections is consistent with the sexual deception pollination syndrome. Also consistent with sexual deception is the constancy of visitation to only one orchid species. Coleman (1932) found that male *L. lanarium* ignored flowers of *D. sulphurea* when placed in a jar with them, but quickly visited and removed pollinaria from those of *D. behrii* when they were introduced. Nash (1979) noted that *L. lanarium* was only found in flowers of *D. behrii* in the field despite the presence of other flowering *Diuris* species in the area, including *D. pardina* (as *D. maculata*), *D. orientis* D. L. Jones (as *D. longifolia* R.Br.) and *Diuris* × *palachila* R.S. Rogers.

However, other aspects of the pollination mechanism of *Diuris behrii* are not typical of sexual deception. The colour of the flowers is more representative of nectar mimicry, and the labellum shows no sign of insect mimicry. In addition, none of the authors observed any sexual behaviour by the male bees. Rather, Coleman (1932) and Nash (1979) found the bees would push their mouthparts into the narrow space between the base of the labellum and column as if attempting to reach a deep source of nectar. Indeed, dissections of flowers by D. L. Jones (unpublished) have revealed a deep narrow hollow that contains no nectar (but may be probed by bees) in flowers of the *D. behrii* complex.

An unusual feature of the relationship between *D. behrii* and its *Lasioglossum* pollinators is the frequent finding of bees resting motionless in the flowers, sometimes for hours, and even overnight (D. L. Jones, unpublished), often with two or three bees per flower (Coleman 1932; Bates 1977; Nash 1979). Coleman (1932) suggested they may be stupefied, and Bates (1977) considered they were drugged by a narcotic substance in the stigma to allow time for the viscidium to set fully on the frons. However, contrary to Bates (1977), Coleman (1932) and Nash (1979) found the resting bees became active when disturbed and did not seem to be drugged. Nevertheless, no matter what the stimulus, the resting period may be important given the ability of *Lasioglossum* species to remove pollinaria of *D. behrii* as noted above. The resting of bees in *Diuris* flowers is not known to occur in any species other than *D. behrii* (D. L. Jones, unpublished).

The nature of the attraction by *D. behrii* for male *Lasioglossum* bees remains a mystery. The available evidence for sexual deception is weak, and some other mechanism seems more likely. The absence of females in collections may reflect sexual differences in foraging behaviour. For example, Rayment (1935) noted that males of *Trichocolletes venustus* (Colletidae) most frequently visited flowers of *Hovea longifolia* (Fabaceae) for nectar, whereas nesting females visited only *Daviesia* species (Fabaceae) for pollen. *Diuris behrii* may be a floral mimic of species pollinated primarily by male *Lasioglossum.*

Diuris sulphurea was identified as sexually deceptive by Coleman (1933*c*). However, as with *D. behrii*, the evidence is weak. She was unable to catch the pollinator, so the identity and sex of visiting bees is unknown. The assumption of sexual deception is based entirely on the bees' behaviour which resembled that of pseudocopulation by the ichneumonid wasp *L. excelsa* on *Cryptostylis* species, with which Coleman was familiar. Visits to *D. sulphurea* flowers were brief, and the pollinarium firmly adhered without the need for a setting period. The bees did not seem to be feeding but curved their abdomens over the humped labellum in a copulatory manner. Coleman (1933*c*) proposed that the humped labellum and the maroon markings may resemble the shape and colour of the female. The frequency of visits to flowers in the field was low, which is consistent with a deceptive pollination syndrome, whether food or sexual deception. The brevity of the visits by the bee could be explained by the absence of nectar or learned avoidance. More work is needed to unravel the pollination mechanism of *D. sulphurea.*

Hybrids occur relatively commonly among some eastern Australian *Diuris* species (Jones 1970*a,c*; Ulherr 1970*a*; Beardsell 1975; Bates 1978*a*) but are absent in the large Western Australian assemblage (D. L. Jones, unpublished). Occasionally large hybrid swarms involving considerable introgression are formed (Jones 1970*c*), but more usually hybridism is limited to small groups of F_1 plants. It appears that isolating mechanisms among species are incomplete in *Diuris*, leading Jones (1970*c*, 1991) to view the genus as recently evolved and rapidly speciating. Nevertheless, it is clear that introgression is limited because the integrity of the parent species remains largely intact over most of their distributions.

There appear to be two main mechanisms limiting introgression: pollinator specificity (Coleman 1932) and hybrid sterility (Bates 1978*a*; Jones 1988). The discovery of pollinator specificity in *D. behrii* by Coleman (1932) and Nash (1979) indicates that movement of vectors between *Diuris* species may be only occasional. Most hybrids do not backcross with their parents or intercross with each other because their progeny are sterile (Bates 1978*a*). David L. Jones (unpublished) has found that all hybrids involving *D. punctata* and *D. orientis* are invariably sterile, whereas those among members of the *D. chryseopsis* and *D. maculata* groups are fertile. **(CCB)**

Uses

Species of *Diuris* are grown as ornamentals by specialist growers. **(DJ)**

Cultivation

Diuris species that have spaghetti-like tubers are more likely to flower if the clumps of tubers are left attached to each other than if broken up and spread around in the pot. For best flowering, it is better to leave these pots undisturbed for several years.

Mix: basic. Light: 25% shade. Watering: late summer–early autumn until late spring–early summer, depending on the species. Flowering: different species in flower from winter to mid-summer. Mature plants of most species flower well. Some, however, flower well only after a summer fire in the wild, e.g. *D. corymbosa*, and in cultivation good flowering can be difficult to achieve. Propagation: some *Diuris* are colony-formers, but most are solitary species or may make a second tuber if robust. *Diuris* respond well to tuber removal or can be propagated from seed sown around parent plants. **(HR)**

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36. ORTHOCERAS

Orthoceras R.Br., *Prodr.*, 316 (1810). Type species: *Orthoceras strictum* R.Br.

Derivation of name

From the Greek *orthos*, straight, and *keras*, horn, which reflects the horn-like character of the lateral sepals. **(DJ)**

Description (Plate 41; Fig. 36.1)

Perennial geophytic *herbs*. *Roots* filamentous. *Tubers* ovoid to ellipsoid, paired, fleshy, naked; replacement tubers produced on the end of short droppers; daughter tubers absent. *Stem* erect, short, unbranched, terete, with membranous cataphylls at each node. *Leaves* basal, 2–6 per shoot, spirally arranged, sessile; lamina much longer than wide, erect, convolute in bud, conduplicate, margins entire; venation anastomosing. *Inflorescence* racemose, 1–many flowered, erect, terminal; scape wiry, with 1–3 sterile bracts, the lowest bract often extended and leaf-like; floral bracts foliaceous, sheathing. *Flowers* resupinate, dull-coloured, sessile; perianth firm and fleshy. *Dorsal sepal* free, shorter and broader than the lateral sepals, concave, cucullate. *Lateral sepals* free, filiform–terete, projecting as spreading to erect horns. *Petals* free, much smaller and markedly dissimilar to the sepals, hidden by the dorsal sepal, bilobed or unequally emarginate. *Labellum* free, attached by its base to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina strongly three lobed, curved; lateral lobes erect and incurved, closely flanking the column; mid-lobe flat, recurved, the distal margins entire; callus consisting of either a basal ridge or two basal swellings more or less connected to a mound on the anterior side; nectar absent. *Column* with stamen and style almost completely free, very short; wings narrow, fused only at the base, papillate, erect and flanking the filament and style; column foot absent; anther dorsal, erect, two-celled, persistent, basifixed; pollinarium present, consisting of two pollinia attached directly to a viscidium; pollinia clavate, mealy, cream; viscidium dorsal; rostellum apical; stigma entire, large, circular. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, thin-walled, glabrous, erect. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 36.2)

Orthoceras comprises one to three species distributed in Australia, New Zealand, and New Caledonia. **(DJ)**

Palynology

Pollen of *Orthoceras strictum* R.Br. is 28 μm; inaperturate; and strongly reticulate (Erdtman 1952). **(AP)**

Ecology

Orthoceras, which is distributed between about 21°30′ south in New Caledonia and about 42° south in Tasmania, grows as solitary individuals or in loose groups, reproducing solely from seed. In Australia *Orthoceras* occurs in moist grassy habitats, heathland and sclerophyll forests, mostly in the lowlands but extending up to about 700 m. In New Caledonia it grows in maquis on ultrabasic soils, and in New Zealand it has been recorded from lowland clay banks and road embankments in forests. Plants are dormant over

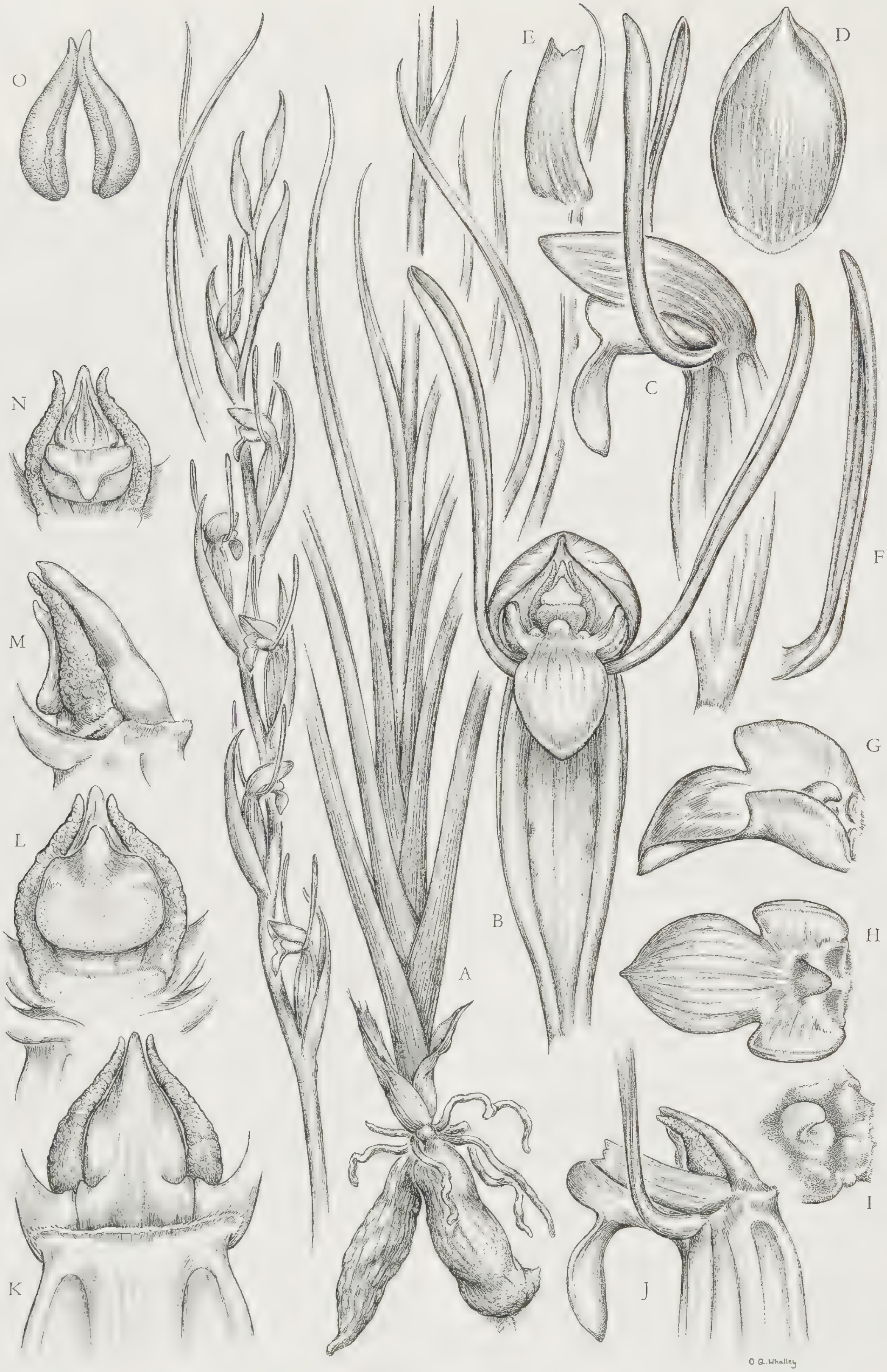

Fig. 36.1. *Orthoceras strictum* R.Br. A. Habit, ×1; B. Flower from front, ×4.5; C. Flower from side, ×4.5; D. Dorsal sepal, ×4.5; E. Petal, ×4.5; F. Lateral sepal, ×4.5; G. Labellum from side, ×6; H. Labellum from above, ×6; I. Labellum, enlargement showing callus, ×9; J. Flower from side (dorsal sepal removed), ×4.5; K. Column from behind, ×9; L. Column from front, ×9; M. Column from side, ×9; N. Column from front (apex of stigma folded down), ×6; O. Pollinia, ×9. Drawn by Oliver Q. Whalley from Kew Spirit Collection no. 45712.

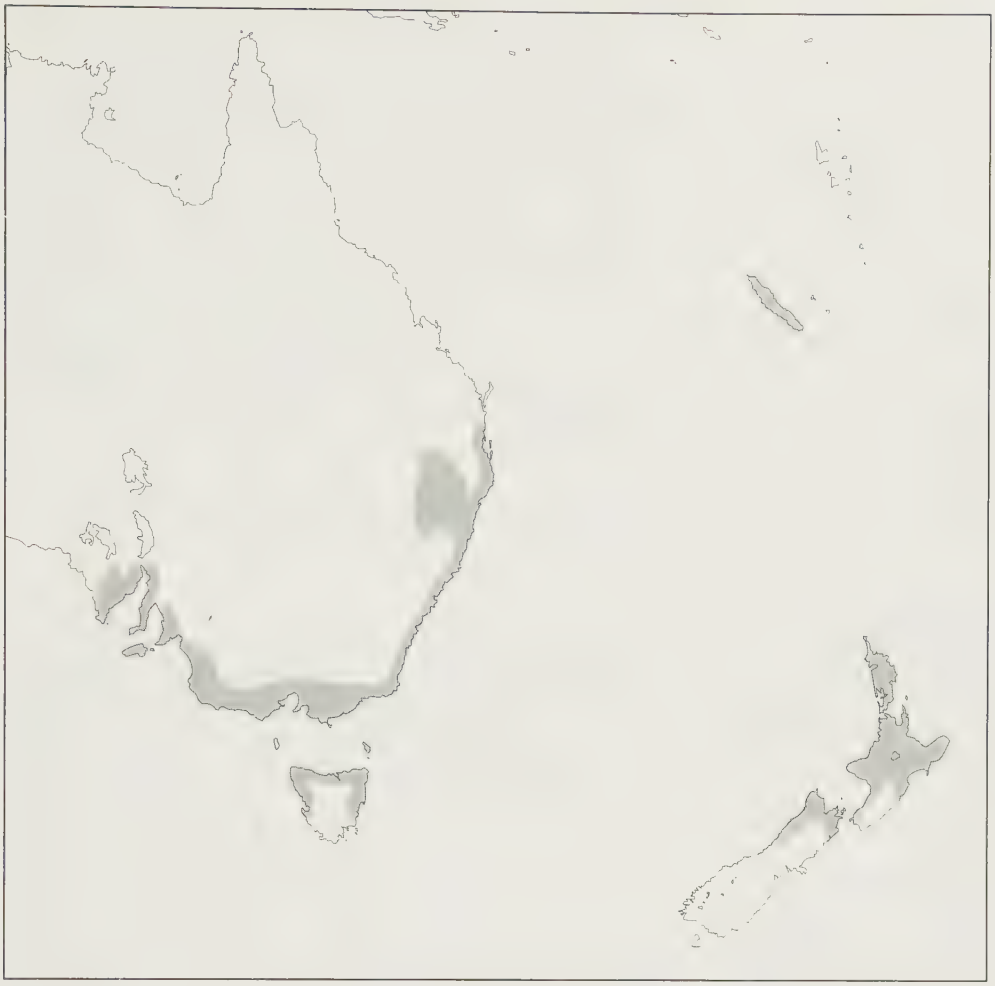

Fig. 36.2. Distribution map of *Orthoceras*.

late summer, grow actively in late autumn and winter, and flower in late spring to early summer. Dispersal of seed begins 8–12 weeks after pollination. **(DJ)**

Pollination

Orthoceras species are obligately self-pollinating with no opportunity for outcrossing (Fitzgerald 1877; Rogers 1913; Molloy 1990). Fitzgerald (1877) and Rogers (1913) studied the mechanism of autogamy in *Orthoceras strictum* in detail.

Orthoceras strictum has a column similar to that of *Diuris*—short, with the stigma opposite the base of the labellum and the anther behind the stigma. A prominent rostellum is present in the upper margin of the stigma in front of the apices of the two anther cells. Two column wings flank either side of the stigma. The labellum has a prominent rounded callus at the base.

Fitzgerald (1877) found that all flowers of *O. strictum* set seed in the field, but none had pollen on the stigma nor were their pollinia removed. He also found that the rostellum was non-functional; the pollinia did not become attached to it and could not be removed by an insect visitor. However, if the pollinia were removed from the anther cells, the seed failed to develop; but if the removed pollinia were placed on the front of the stigma, normal seed development occurred. He found that in undisturbed flowers the pollinia became attached to the back of the stigma, the wall of which thinned, allowing pollination to occur.

Rogers (1913) expanded on Fitzgerald's findings. He found the surface of the anther cells directly behind the stigma began to split in the late bud stage revealing the moderately friable pollinia within. This dehiscence was complete at anthesis at which time the pollinia were united at their apices and hung on either side of the septum separating the two anther cells. No connection to the rostellum was established. As the flower matured the rostellum bent forward slightly and the pollinia fell forward onto either side of a medial ridge at the back of the stigma. The column wings helped to hold the pollinia in place.

The pollinia began to adhere to the back of the stigma soon after falling. Rogers (1913) concluded that rather than thinning, the back of the stigma softened, and some of the pollen grains germinated through the softened tissue. The growth of numerous pollen tubes through the back of the middle third of the stigma firmly attached the pollinia. After fertilization the labellum rose up in front of the column, pressing the callus into the front of the stigmatic cavity and compressing it against the pollinia. At the same time the dorsal sepal descended, sealing the flower. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Plants of *Orthoceras* are not successful in cultivation and die after 2–3 years. **(HR)**

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SUBTRIBE DRAKAEINAE

Drakaeinae Schltr., *Bot. Jahrb. Syst.*, **45**, 381 (1911). Type: *Drakaea* Lindl.

Tribe Geoblasteae Barb. Rodr. subtribe Chiloglottidinae Szlach., *Fragm. Flor. Geobot., Suppl.* **3**, 23 (1995). Type: *Chiloglottis* R.Br.

Tribe Geoblasteae Barb. Rodr. subtribe Caleaninae Szlach., *Fragm. Flor. Geobot., Suppl.*, **3**, 24 (1995). Type: *Caleana* R.Br.

Tribe Geoblasteae Barb. Rodr. subtribe Drakaeinae (Schltr.) Szlach., *Fragm. Flor. Geobot. Suppl.*, **3**, 24 (1995). Type: not designated.

Description

Tuberous, mostly glabrous, geophytic *herbs*. *Tubers* globose or ovoid, naked. *Leaf* either absent, solitary, distichously paired or up to six spirally arranged in a rosette, encircling the scape or on a lateral growth, convolute, sessile, erect to prostrate. *Inflorescence* single-flowered or racemose. *Flowers* resupinate or non-resupinate, dull-coloured; tepals subsimilar. *Labellum* hinged at the base and passively motile or actively motile on the end of an elastic strap; lamina entire, often with a highly modified insectiform callus; nectar absent. *Column* lacking free filament and style; column foot present; pollinarium usually absent, pollinia four. *Fruit* a dehiscent capsule. **(DJ)**

Anatomy

Leaf

SURFACE

Papillae, one per cell, on both surfaces in *Caleana major* and adaxially in *Drakaea* (limited to margins in *D. livida* and *D. thynniphila*). Cuticle sculpturing striate in *Caleana*; striate-anastomosing in *Arthrochilus*; crinkled in *Chiloglottis*; smooth, punctate to striate in *Drakaea*; and smooth in *Spiculaea*. Epidermis: cells elliptical to polygonal and axially elongated on abaxial surface of *Caleana*. Anticlinal walls thick with conspicuous pit-fields, sinuous abaxially in *Arthrochilus*, *Caleana nigrita*, and *Drakaea*. Stomata on both surfaces, except restricted to abaxial surface in *Drakaea*. Size ranges, mean dimensions, and mean length: width ratios of guard-cell pairs provided in Pridgeon (1994*b*).

TRANSECTION

Cuticle thin, sculpturing as above. Epidermis: cells isodiametric, elliptical to polygonal, the outer wall differentially thickened (inner wall as well in *Caleana*). Adaxial cells appreciably larger than abaxial cells in *Arthrochilus* and *Chiloglottis*. Stomata superficial, substomatal chambers shallow. Mesophyll heterogeneous, up to six palisade layers in *Spiculaea*, in all taxa except *C. trapeziformis* and *C. trilabra*. Vascular bundles as for the tribe. Bundle-sheath bilayered in *Drakaea*. Ergastic substances: raphide bundles in mesophyll idioblasts of all taxa except *Spiculaea*. Brownish aggregations surrounded by a transparent sheath, not birefringent in polarized light, in most epidermal cells of *Spiculaea*.

Collar/stem

TRANSECTION

Hairs on collar multiseriate, associated with mycorrhiza in *Arthrochilus*, *Chiloglottis*, and *Spiculaea*; uniseriate, the apical cell supported by a buttress of 4–5 epidermal cells in *Caleana* and *Drakaea* (Pridgeon, 1994*a*). Cuticle thin, smooth to minutely striate or rugose. Epidermis: cells elliptical, rectangular to polygonal, the outer wall usually thickened. Stomata present or absent depending on the taxon. Ground tissue of collar parenchymatous, often infected with hyphae and pelotons. Chlorenchyma dense in the leafless species *A. huntianus*. Inner layers of cortex of *Arthrochilus* and

Artificial key to the genera of Drakaeinae (DJ)

1. - Leaf solitary at the base of the scape 3
   - Leaves either absent or 2 or more at the base of the scape or on a separate lateral growth 2
2. - Leaves 2, distichous; flower solitary, resupinate; column foot vestigial; column wings entire .... **39. *Chiloglottis***
   - Leaves either absent or 3 or more spirally arranged in a lateral rosette (rarely stem-encircling); flowers few to many, non-resupinate; column foot prominent; column wings bilobed .... **37. *Arthrochilus***
3. - Labellum actively motile, attached by a thickened sensitive strap; labellum lamina glabrous or with warty glands; column wings entire, broadly expanded, adnate to the column foot .... **38. *Caleana***
   - Labellum passively motile, hinged by a short membranous strap; labellum lamina with branched trichomes; column wings lobed, narrow, not adnate to the column foot 4
4. - Leaf thick and spongy; flower solitary; column wings with a single lobe; column foot long and prominent .... **40. *Drakaea***
   - Leaf thin to leathery but not thick and spongy; flowers several; column wings bilobed, the upper lobes flanking the anther 5
5. - Leaf leathery, usually withered at anthesis; column foot vestigial .... **41. *Spiculaea***
   - Leaf thin-textured, extant at anthesis; column foot long and prominent .... **37. *Arthrochilus***

Caleana sclerotic, forming a sclerenchyma sheath. Endodermis of collar: cells elliptical to polygonal. Vascular bundles collateral, usually arranged in 1–3 rings. Xylem tracheids with annular, helical, scalariform, or pitted thickenings. Crystals: raphide bundles or rod-shaped crystals in ground tissue observed in all taxa except *Spiculaea.*

Tuber

TRANSECTION

Hairs absent in most taxa; multiseriate, associated with mycorrhiza in *A. huntianus*; unicellular, filamentous, nonglandular in *A. sabulosus.* Velamen 1–3 layered, cells elliptical to polygonal, somewhat compressed periclinally; outer and/or radial walls infrequently thickened; cells in *D. livida* pitted. Exodermis: cells rectangular, elliptical to polygonal; walls of uniform thickness or thicker on outer and/or radial walls, depending on species. Ground tissue parenchymatous, filled with starch grains; outer layers in *A. huntianus* infected with hyphae and pelotons. Endodermis: cells elliptical to polygonal. Stele medullated, 4–14 arch, depending on species; dissected into nine discrete strands in *A. huntianus.* Xylem tracheids with scalariform or pitted thickenings. Ergastic substances: starch grains and raphides in ground tissue.

Root

TRANSECTION

Hairs multiseriate, associated with mycorrhiza, in *A. huntianus* and *Spiculaea*; hairs in other taxa unicellular, from outermost velamen layer. Velamen 1–2 (–3) layered, cells rectangular to polygonal; walls of uniform thickness or outer wall thickened, depending on taxon. Walls with reticulate thickenings in *Drakaea* and with pores in a reticulate pattern in *Spiculaea.* Exodermis: cells rectangular to polygonal, walls of uniform thickness or outer wall thickened. Cortex parenchymatous, outer layers infected with hyphae and pelotons, innermost layers occasionally with starch grains. Cortical cells in *Drakaea* with reticulate wall thickenings. Endodermis: cells elliptical to polygonal. Stele medullated, 3–10 arch; pith sclerotic in *C. trilabra.* Xylem tracheids with helical, scalariform or pitted thickenings. Crystals: raphide bundles in cortex of some species. **(AP)**

Phylogenetics

Subtribe Drakaeinae was created by Schlechter to encompass those Australasian terrestrial genera with winged columns, as distinct from Pterostylidinae in which the petals and dorsal sepal form a galea (Schlechter 1926). Previous classifications placed *Caleana*, *Chiloglottis*, and *Drakaea*, assigned by Schlechter to Drakaeinae, either in Caladeniinae (Lindley 1840; Dressler 1974, 1981, 1993) or Pterostylidinae (Pfitzer 1889). Recent embryological (Clements 1995) and molecular analyses (Clements *et al.*, in prep; Kores *et al.* 2000) confirm the distinctiveness of these genera from Caladeniinae or Pterostylidinae (the latter of which are not members of Diurideae). **(MAC)**

37. ARTHROCHILUS

Arthrochilus F. Muell., *Fragm.* **1**, 42 (1858). Type species: *Arthrochilus irritabilis* F. Muell.

Drakaea Lindl. sect. *Akaedra* Schltr., *Bot. Jahrb. Syst.* **45**, 383 (1911). Type species: *Drakaea irritabilis* Rchb.f. and *D. huntiana* F. Muell.

Derivation of name

From the Greek *arthron*, joint, and *cheilos*, lip, referring to the jointed labellum of these orchids. **(DJ)**

Description (Plate 42; Fig. 37.1)

Perennial geophytic *herbs. Roots* filamentous. *Tubers* present or reduced to small protocorm-like structures (*A. huntianus*), ovoid,

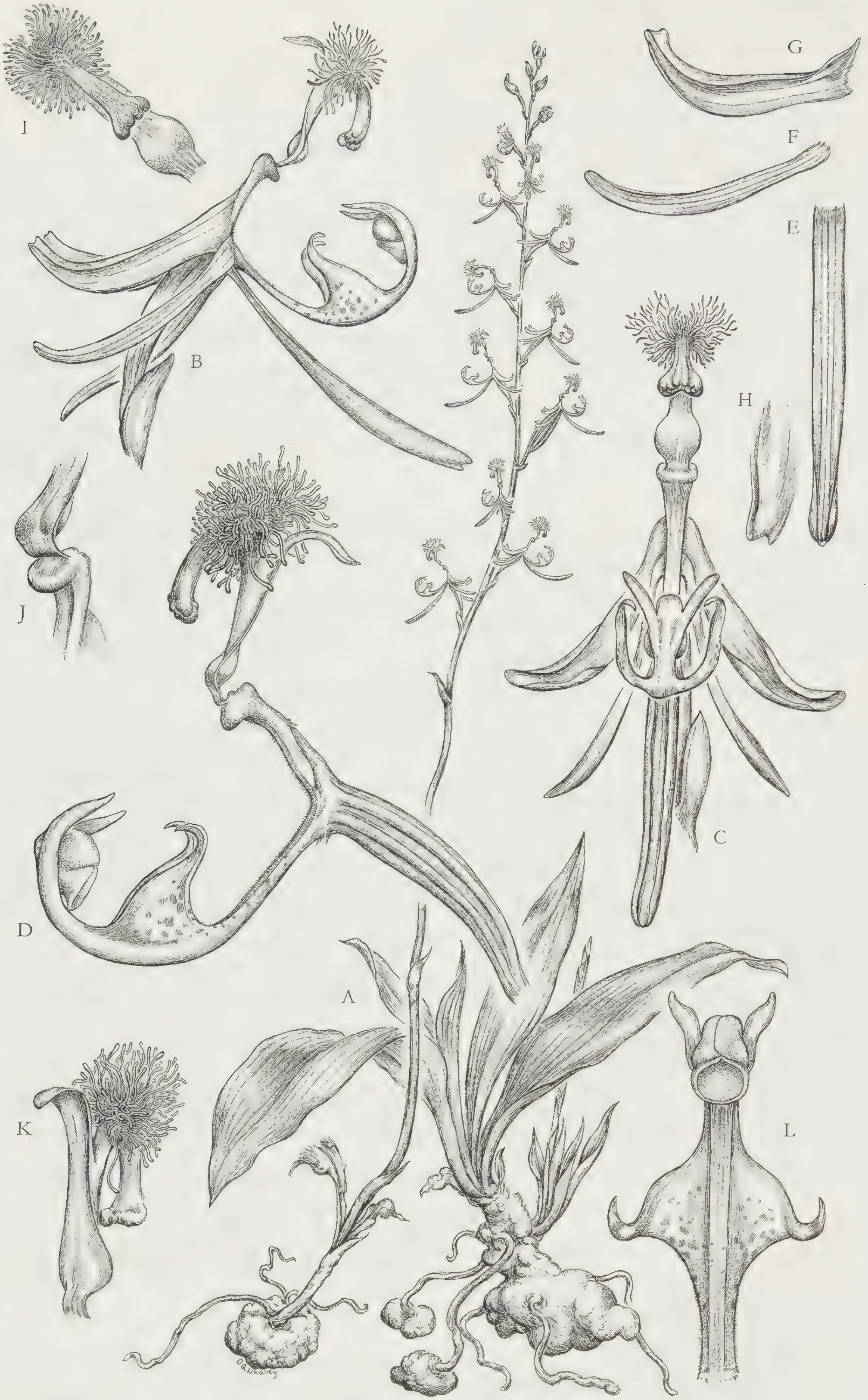

Fig. 37.1. *Arthrochilus prolixus* D.L. Jones, ×1; B. Flower from side, ×6; C. Flower from front, dorsal sepal bent forward ×6; D. Flower from side, sepals and petals removed, ×9; E. Dorsal sepal, ×6; F. Petal, ×6; G. Lateral sepal, ×6; H. Lateral sepal from side, apex, ×6; I. Labellum from above, ×7.5; J. Articulation between column foot and claw, ×12; K. Labellum, oblique view, ×7.5; L. Column from front, ×9. Drawn by Oliver Q. Whalley from Kew Spirit Collection no. 51632 with reference to W. H. Nicholls (1969), for habit.

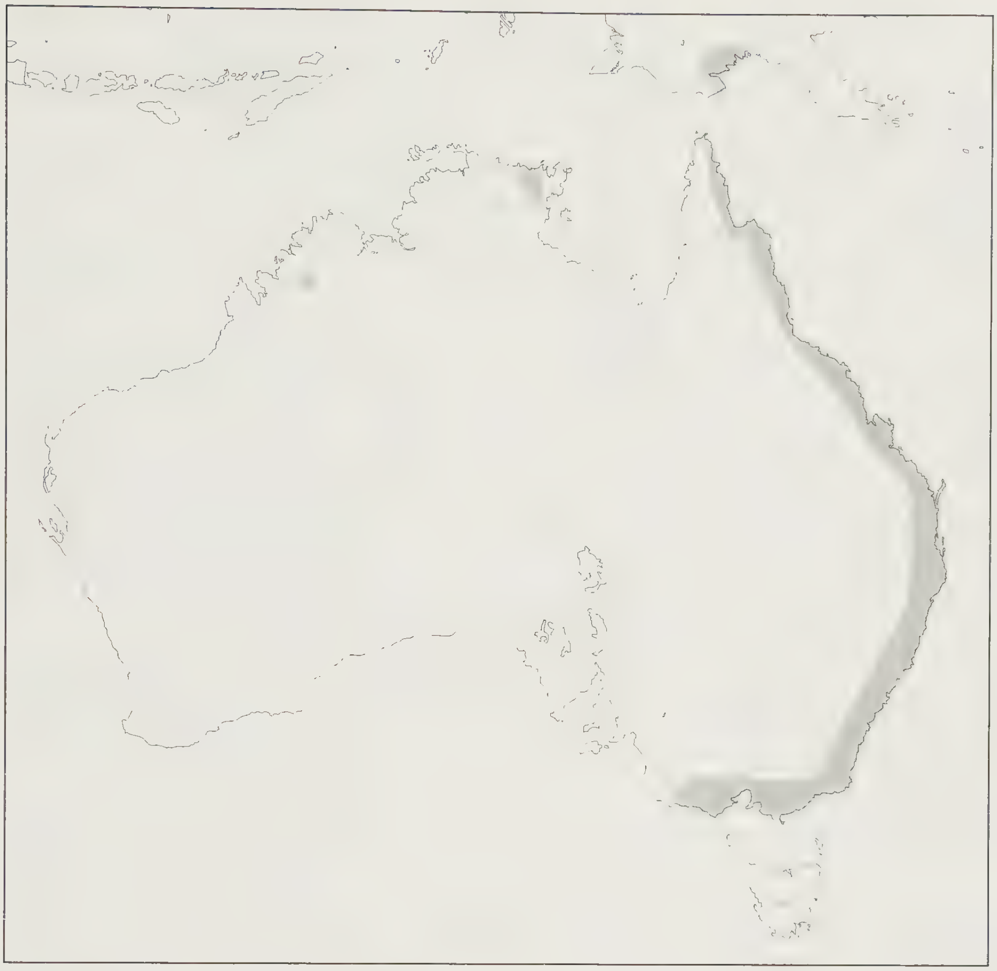

Fig. 37.2. Distribution map of *Arthrochilus*.

solitary, fleshy, naked; replacement tubers present or absent; daughter tubers formed on the end of slender root-like stolons or absent. *Stem* erect, short, unbranched, with membranous cataphylls at each node. *Leaves* either absent (*A. huntianus*), basal and stem-encircling or on a lateral growth arising from the base of the scape, single or 2–6 in a rosette, shortly petiolate to subsessile; lamina mostly longer than wide, convolute in bud, margins entire, hypostomatic; venation anastomosing; petiole grooved adaxially. *Inflorescence* racemose, few–many flowered, erect, terminal; scape wiry, with many sterile bracts; floral bracts reduced, semi-sheathing. *Flowers* non-resupinate, dull-coloured, shortly pedicellate; small columnar papillae massed on the bases of the perianth and anterior surface of the column. *Dorsal sepal* free, similar to or larger than the lateral sepals, recurved. *Lateral sepals* mostly free, anteriorly decurrent on the column foot. *Petals* free, narrower than the sepals. *Labellum* free, hinged to the underside of the column foot by a claw, appearing as an insectiform lure, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina almost vestigial, lorate, not lobed, base swollen; callus dominating the labellum, proximally fused to the lamina, distally free and ornamented with warts, plumose cilia and shiny clavate calli; nectar absent. *Column* elongate, with two pairs of elongate, incurved, unequal, wing-like projections, the larger one situated medially, the smaller one projecting over the anther; column foot short or long, swollen into an apical knob or entire; anther terminal, four-celled, persistent, basifixed, porrect; pollinarium present (*A. huntianus*) or absent; pollinia four, bilobed, flat, mealy, yellow; viscidium present (*A. huntianus*) or absent; rostellum ventral; stigma entire, circular, concave. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, glabrous, erect; sepals and petals persistent; pedicels elongating in fruit (*A. huntianus*) or not. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 37.2)

A genus of about 10 species distributed in south-eastern and north-eastern Australia and Tasmania, including Torres Strait islands and southern Papua New Guinea. **(DJ)**

Ecology

Arthrochilus is a small, highly specialized genus that reaches its greatest development in tropical areas of eastern Australia, with elements extending through the Torres Strait islands into south-western Papua New Guinea. Two species, including the leafless saprophyte *A. huntianus*, occur in south-eastern Australia.

Latitudinally the leafy members of *Arthrochilus* are distributed from about 8° south in the Fly River region of Papua New Guinea to about 33°50′ south in the northern suburbs of Sydney. *Arthrochilus huntianus* subsp. *huntianus* occurs from about 33°40′ south in the Blue Mountains west of Sydney to about 38°45′ south on the mainland in southern Victoria, with subsp. *nothofagicola* D. L. Jones occurring disjunctly at about 43° south in Tasmania.

With the exception of *A. huntianus*, which grows individually and in small loose groups, all other species of the genus reproduce vegetatively to form clonal colonies. Daughter tubers are produced on the end of root-like stolons, which can sometimes be surprisingly long. All of these colony-forming species flower and grow actively in the summer. In members of the *A. irritabilis* alliance the inflorescence emerges long before the leaves, which appear later in a rosette arising on a lateral growth from the base of the scape, or, in *A. rosulatus* D. L. Jones, encircling the base of the scape. Non-flowering plants develop a rosette only. In *A. byrnesii* Blaxell and *A. dockrillii* Lavarack the single leaf, which is basal, is well developed before the inflorescence emerges. Growth in all of these species is closely tied in with the monsoonal wet season. Seeds are released rapidly in the tropical species, usually within 6–10 weeks of pollination. In these species flower production continues as long as favourable growing conditions persist, and the inflorescences can become tall with all stages present, from immature buds to dehisced capsules. In *A. huntianus* flowering is much more limited, and capsules take 8–12 weeks to dehisce.

Most of the leafy species of *Arthrochilus* are distributed in lowland regions with *A. oreophilus* D. L. Jones the exception, occurring in ranges and tablelands at about 1000–1200 m. Habitats include forest, woodland, and heathland. These orchids commonly grow in sandy soils, which may be either well-drained or seasonally wet. *Arthrochilus huntianus* ranges from the lowlands to montane and subalpine regions and grows mainly in forests and woodlands, often in relatively bare areas among accumulations of litter. *Arthrochilus huntianus* subsp. *nothofagicola* has a restricted distribution and is known from tall forest with a rainforest and tree fern understorey. **(DJ)**

Pollination

The remarkable pollination mechanisms of *Arthrochilus* species rely on the sexual deception of male thynnine wasps (Rotherham 1967; Cady and Rotherham 1970; Stoutamire 1981). All species have highly modified insectiform labella mimicking the shape of a flightless female wasp. The labellum is attached to an extended column foot by a flexible hinge, about which it can be moved by the insect against the column. Also unusual in *Arthrochilus* are the hook-like column wings that perform an important role in manipulating the pollinator.

In most *Arthrochilus* species the labellum lamina is divided into distinct regions representing the different body parts of the female thynnine being mimicked. There is usually a prominent basal pseudo 'head' region and narrow 'neck' fashioned from a large stalked callus. The 'neck' region of the decoy probably mimics the slender thorax of the thynnine female (Plate 42). The main part of the labellum has either a further large callus or a diffuse arrangement of hairs representing the insect's body. In *A. huntianus* the head of the basal callus is divided into two eye-like projections, and apical to the narrow neck is an intermediate callus.

Rotherham (1967) observed and photographed the pollination of *A. huntianus*. From the photograph he made an excellent drawing of the position of the *A. huntianus* pollinator on the labellum when pollination occurs. The wasp grasped the pseudofemale around the thorax just behind the head with its forelegs and the rest of the body with its other pairs of legs, as it would a real female. He believed that the momentum of the wasp landing on the labellum caused it to swing toward the column, directing the insect between the hooked wings where the pollinia were deposited on its thorax. Stoutamire (1981) on the other hand reported that the pollinator of *A. huntianus* attempted to fly away with the decoy, causing it to swing into the column, removing the pollinia.

Rotherham's (1967) and Stoutamire's (1981) observations provide only a partial picture of the pollination mechanism of *Arthrochilus*. The floral structure of *Arthrochilus* species, particularly *A. huntianus*, is similar to that of *Spiculaea ciliata* (*q.v.*) and is likely to have a similar pollination mechanism. The following account of the pollination mechanism of *Arthrochilus* combines the published information on *Arthrochilus* and *Spiculaea* and is supplemented by unpublished observations of A. Logan and C. Bower.

The swinging labellum of *Arthrochilus* utilizes the behaviour of many thynnine male pollinators that immediately fly upward after grasping the wingless female. As it lifts the labellum decoy, the male is swung headlong against the column. In *A. huntianus* the male grasps the hanging decoy from below and, as he attempts to fly away, the labellum swings upward toward the column, and the bases of his beating wings are caught by the column hooks. The trap comprises two pairs of projecting column appendages: a straight pair projecting outward from the top of the column and a hooked pair originating below the stigma, which curves upward, almost meeting the upper pair about halfway along their length. The male's wings first slide along the straight appendages, the momentum forcing them past the ends of the curved pair. When the wasp comes to rest against the column, the curved pair of appendages holds the wing bases, preventing a quick escape. Thus detained, the male is correctly positioned to pollinate the flower. The male struggles on the hooks for some seconds, sufficient to allow the viscidium of *A. huntianus* to attach to the thorax before the wasp frees itself by walking backward down the labellum.

Only *A. huntianus* has a viscidium. The other *Arthrochilus* species appear to receive a coating of sticky secretion from the rostellum and raise the one-way anther flaps in a manner similar to most other Drakaeinae and many Caladeniinae. In these species the column appendages are less hook-like and may function more as stops to prevent excessive labellum rotation. Pollinia are removed as the wasp backs out of the trap along the labellum. The labellum decoys of the more northern *Arthrochilus* species are also more compact and less heavily adorned than *A. huntianus*. The violent struggles of the pollinators of tropical *Arthrothynnus* species often tear the labellum from the flower, and it is not uncommon to find whole racemes without labella (D. L. Jones, unpublished).

The pollinators of only three of the ten described *Arthrochilus* species are known. All three are pollinated by male thynnine wasps of the genus *Arthrothynnus* (Brown 1996). *Arthrothynnus huntianus* is the only insect that has been attracted to *Arthrochilus huntianus* in widely dispersed localities on the central and southern tablelands of New South Wales and western Victoria (Brown 1996). Similarly, *Arthrothynnus rufiabdominalis* is the pollinator of *Arthrochilus irritabilis* in south-eastern Queensland (Brown 1996; A. Logan, unpublished), and an undescribed species of *Arthrothynnus* has been attracted to *Arthrochilus latipes* in the Northern Territory (G. R.Brown, unpublished). As yet there are few confirmed pollinator records to assess the degree of pollinator specificity among *Arthrochilus* species. Nevertheless, it appears clear that *Arthrochilus* has adapted to the thynnine genus *Arthrothynnus* for pollination. The identification of the pollinator of *Arthrochilus huntianus* as a species of *Rhagigaster* by Rotherham (1967), confirmed by Cady and Rotherham (1970) and Adams and Lawson (1993), was made from a photograph and is incorrect (Brown 1996). **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Species of *Arthrochilus* are difficult to maintain in cultivation. **(HR)**

Taxonomic literature

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38. CALEANA

Caleana R.Br., *Prodr.*, 329 (1810). Type species: *Caleana major* R.Br.

Caleya R.Br. in Aiton, *Hort. Kew* (ed.2), **5**, 204 (1813) (orth. var.).

Paracaleana Blaxell, *Contr. New South Wales Natl. Herb.*, **4**, 281 (1972). Type species: *Caleana minor* R.Br. (*Paracaleana minor* (R.Br.) Blaxell).

Derivation of name

Honouring George Caley, explorer and botanist in Australia in the late 1700s and early 1800s. Caley had a special interest in orchids and collected the types of many species described by Robert Brown. **(DJ)**

Description (Plates 43, 44; Fig. 38.1)

Perennial geophytic *herbs*. *Roots* filamentous. *Tubers* ovoid, solitary, fleshy, naked; replacement tubers formed on the end of short droppers; daughter tubers formed on the end of root-like stolons. *Stem* erect, short, unbranched, with membranous cataphylls at each node. *Leaf* one, basal, sessile; lamina thin, longer than wide, convolute in bud, margins entire; venation anastomosing. *Inflorescence* racemose, 1–several flowered, erect, terminal; scape wiry, with one small sterile bract; floral bracts reduced, sheathing. *Flowers* non-resupinate, dull-coloured, pedicellate. *Perianth* and column recurved, with the labellum projecting like an insectiform lure. *Dorsal sepal* free, subsimilar to the lateral sepals, recurved. *Lateral sepals* free. *Petals* free, narrower than the sepals. *Labellum* free, hinged to the apex of the column foot by a long, actively irritable claw, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina not lobed, variously folded and curved to resemble the body of an insect, peltately attached to a short basal stalk that is hinged to the apex of the claw; upon contact the lamina folds into the broad column wings; callus apparently absent (*C. major*) or consisting of shiny wart-like calli; nectar absent. *Column* elongate with broad porrect wings fused to the column and column foot, forming an inverted concave structure; column foot short to long; anther terminal, four-celled, persistent, basifixed, rostrate; pollinia four, clavate, flat, mealy, naked, yellow; rostellum ventral; stigma entire, circular, concave. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, glabrous, erect; sepals and petals persistent; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

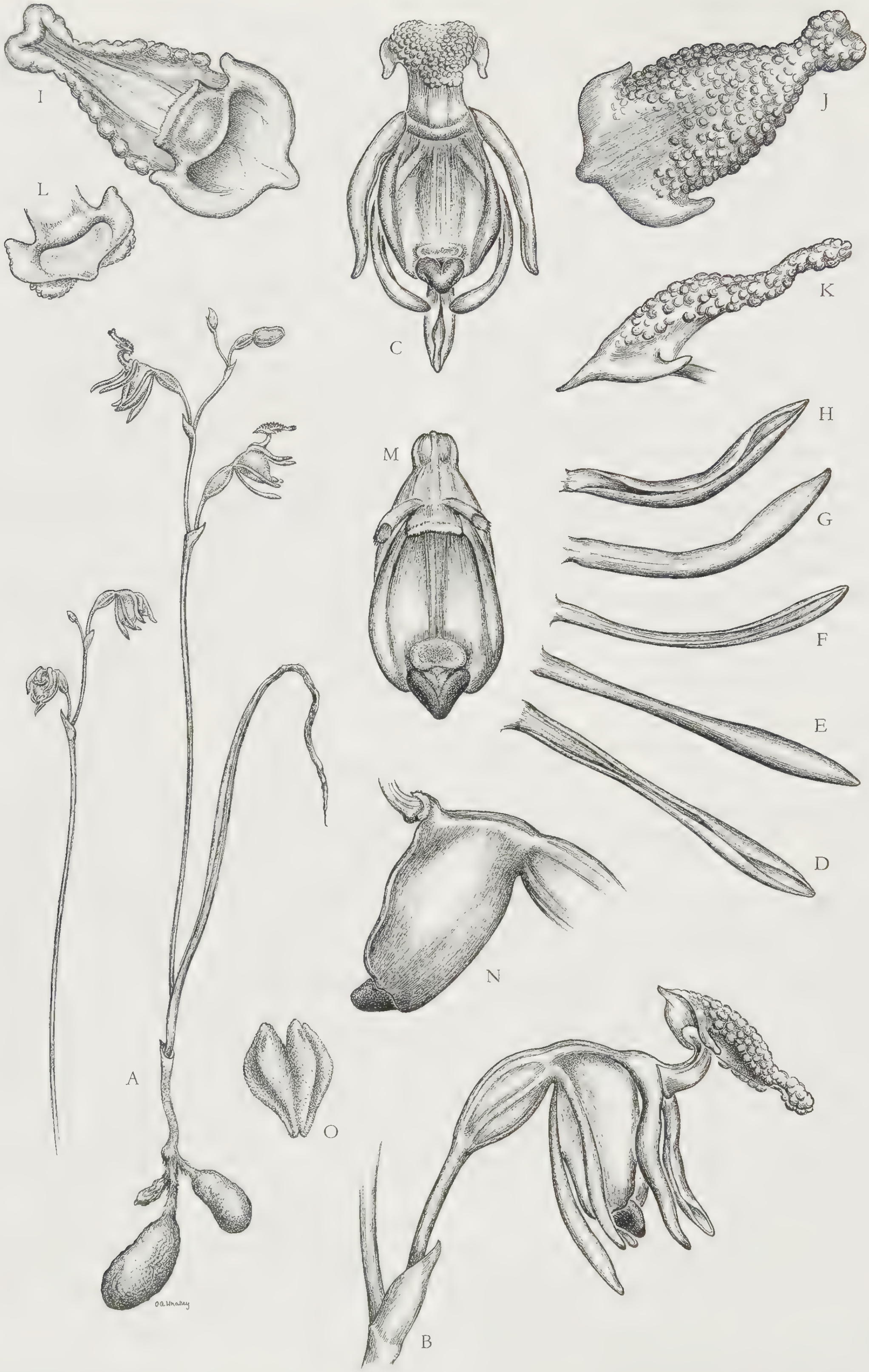

Fig. 38.1. *Caleana minor* R.Br. A. Habit, ×1; B. Flower and bract from side, ×6; C. Flower from front, ×6; D. Dorsal sepal, front, ×6; E. Dorsal sepal, back, ×6; F. Petal, ×6; G. Lateral sepal, back, ×6; H. Lateral sepal, front, ×6; I. Labellum from below, ×9; J. Labellum from above, ×9; K. Labellum from side, ×9; L. Labellum apex, ×6; M. Column from front, ×6; N. Column from side, ×6; O. Pollinia, ×9. Drawn by Oliver Q. Whalley from Kew Spirit Collection nos. 36829, 56232, and 55532.

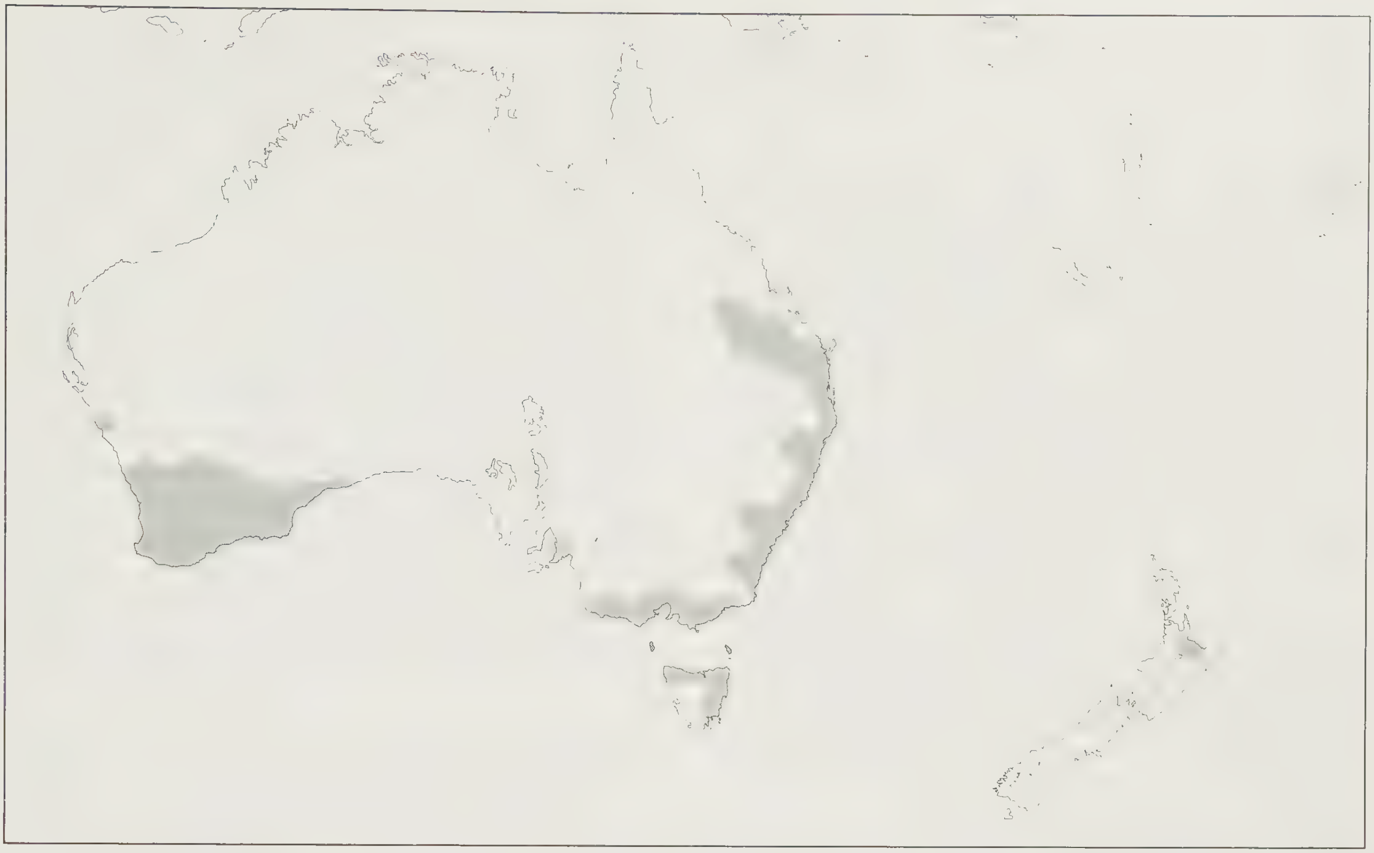

Fig. 38.2. Distribution map of *Caleana.*

Distribution (Fig. 38.2)

A genus of about seven species, six endemic in Australia with one extending to New Zealand. **(DJ)**

Palynology

Tetrads of *Caleana major* are tetrahedral, *c.* 20 μm; inaperturate; tectate-perforate tending to semitectate equatorially; foveolate distally tending to fossulate-reticulate equatorially; the units globose-spherical (Ackerman and Williams 1981). **(AP)**

Ecology

Caleana, which is a remarkable genus renowned for its bizarre flowers and the active motility of its labellum, has developed primarily in Australia but includes a single species, *C. minor*, also occurring in New Zealand where it probably established as a casual migrant from wind-blown seed originating in New South Wales. In eastern Australia *Caleana* is distributed between about 25° south in central Queensland and about 43° south in southern Tasmania; in Western Australia it occurs between about 27° south and 35° south. All species are terrestrials that reproduce from seed and also grow in clonal tufts or colonies. They occur in areas that have a strongly seasonal climate, the plants growing actively in autumn and winter, flowering during spring and early summer, and existing as dormant tubers during the worst excesses of mid to late summer. The leaves of all species are fully developed well before the emergence of the inflorescence, and in many species the leaves may have started to senesce at or before anthesis. Seed dispersal begins 8–12 weeks after pollination.

Caleana species are distributed from mesic habitats to semi-arid regions. The majority of species are found in lowland situations, but *C. major* and *C. minor* extend to about 800 m in the ranges and tablelands of south-eastern Australia. Eastern species commonly grow in open forest, woodland, and heathland, whereas in Western Australia they are more usually found in shrubland, sandplain heath, in shallow soil over granite sheets, and in sandy soil around depressions that are damp to wet in winter. In New Zealand *C. minor* occurs in areas of geothermal activity growing in light to dense scrub on dry sand or clay hills. **(DJ)**

Pollination

The odd-looking, duck-shaped flowers of *Caleana* testify to a unique and peculiar pollination mechanism. The labellum comprises the duck's 'head' mounted on an irritable strap-like 'neck' attached to the base of the column. The duck's 'body' comprises greatly expanded column wings that form a large bowl-like structure around the column. *Caleana* flowers are adapted to trap insects for pollination in an extraordinary mechanism whereby the labellum suddenly flips over into the column bowl, pinning the insect upside down against the column. This action can be triggered manually by lightly pushing down on the glandular apex of the labellum.

There have been no formal studies of the mechanism of labellum movement in *Caleana* or in the unrelated *Pterostylis*, which seems to have a similar process. The following observations were made by the author (C. Bower, unpublished). The strap-like labellum claw has cable-like thickenings running down the sides of the thinner, broad, flexible lamina. In the resting position the lamina has a margin-to-margin concavity, and the claw is bent upward. Slight pressure on the labellum apex bends the strap outward, causing the concavity to evert suddenly, bending the claw rapidly downward.

Triggering the labellum takes place in two stages. Reversal of the claw begins at the outer end, where it joins the labellum, and proceeds rapidly to the basal end. Reversal in the outer three quarters of the lamina tips the labellum under and closely parallel to the claw. It is not until the final quarter of claw reversal that the labellum rotates against the column. This double action ensures that the tip of the labellum clears the column apex. The process is difficult to observe by eye when the labellum snaps shut but can be followed in its slow repositioning.

The rapid movement of the labellum against the column appears to be a mechanical process, whereas the slow resetting indicates a physiological action. Once the labellum returns to its resting position, it is insensitive to triggering for at least 15 minutes (Bates 1989*a*), suggesting a physiological adjustment is needed to reestablish the critical equilibrium.

There have been very few documented observations of pollination in *Caleana*. Cady (1965) reported the pollination of *C. major* by a male sawfly, *Lophyrotoma leachii*. The sawfly landed on top of the bulbous 'duck head' facing the 'duck bill' apex and was thrown against the column, where it remained motionless for 15–20 seconds, apparently stunned, with its thorax pressed against the stigma and anther. It then struggled to free itself for about 90 seconds during which the pollinia were placed on the centre of its thorax, and some of the friable pollen was smeared on the stigma. Cady (1965) argued that the sawfly could pollinate a second plant if it repeated the process. He speculated that the sawfly was using the orchid as a landing platform.

The precise mechanism of pollinia removal from the anther of *Caleana* species is likely to be the same as for other Drakaeinae and the Caladeniinae that all have very similar column structures. To escape, the insect must back out of the enclosing bowl. If the insect's thorax had not already been pressed into the stigma by the initial action of the labellum, it would contact it as it backed out, effecting pollination if it were carrying pollinia. Its thorax would then be coated in glue by the rostellum before lifting the one-way anther flaps and contacting and removing one or more of the pollinia. Cady and Rotherham (1970) suggested incorrectly that *C. major* has a viscid disc and that stunning the pollinator allows time for the glue to set on the thorax.

Bates (1978*b*) noted that sprung flowers of *C. major* in the field in South Australia were almost invariably empty and suggested the wind may often trigger them. The only insects he found trapped in *C. major* flowers were two buprestid beetles, one with pollinia on its head. As the flowers do not secrete nectar or odour, he speculated that the beetles may have been attracted to the smooth, beetle-shaped labellum.

However, Bates (1989*a*) later concluded that *Caleana* was pollinated by sexual deception. This was supported by his observation of the pollination of *C. major* by a male sawfly, *Pterygophorus* sp., near Wauchope in New South Wales (Bates 1989*a*). The process was the same as observed earlier by Cady (1965) with pollinia being placed on the centre of the thorax. The pollinators approached the flowers from downwind, indicating they were following an odour trail in agreement with the behaviour of other sexually deceived pollinators. The flowers of *Caleana* are also dull green, maroon, and brown in colour like most sexually deceptive species in Australia (Stoutamire 1983). However, Bates (1989*a*) collected only one pollinator, and no specific observations of sexual behaviour were noted, so the conclusion of sexual deception must be considered provisional.

Caleana major is the only orchid thought to be pollinated by sexual deception of male sawflies. Whether or not only a single species of pollinator is involved, as suggested by Bates (1989*a*), remains to be determined. Certainly two names of male sawflies, *Lophyrotoma leachii* and *Pterygophorus* sp., exist in the literature (Cady 1965; Bates 1989*a*). *Lophyrotoma* and *Pterygophorus* are sister genera (MacDonald and Ohmart 1993), and the placement of some species is uncertain (J. M. McDonald unpublished). It is possible that the *Pterygophorus* sp. of Bates (1989*a*) and *Lophyrotoma leachii* are the same taxon, but more work is needed to confirm this hypothesis.

Bates (1978*b*, 1989*a*) noted that seed capsules are rarely observed in *C. major* in the field and that pollinators are very difficult to attract by baiting. However, *C. major* is relatively widespread and may be common in some localities. Bates (1989*a*) suggested that the longevity of *C. major* flowers, up to two months, may be related to the scarcity of pollinators.

No published information is available on the pollination of the small duck orchids, included in *Paracaleana* by some authors, except that Hoffman and Brown (1992) state they are pollinated by male thynnine wasps sexually attracted by pheromones emitted from glands on the labellum apex. Baiting trials by the author near Bathurst and Orange in New South Wales (C. Bower, unpublished) showed that *C. minor* is indeed pollinated by small black male thynnine wasps, *Thynnoturneria armiger*, in that area. The pollination mechanism is essentially the same as for *C. major*. The wasps flew upwind to the flowers as if following an odour trail. The males are much longer than the labellum decoy so that when caught the head and thorax are pressed against the column, but the abdomen is free and waves about violently. By contrast to the sawflies on *Caleana major*, backward escape by *Thynnoturneria armiger* was rapid, of the order of only a few seconds.

The labellum of *C. minor* is dark-coloured, glandular, and somewhat insect-like. The decoy is broadest at the base and narrows toward the apex before expanding again into two short eye-like lobes, which probably represent the head region of the female. It is likely the correct orientation of the male is achieved when he grapples the thorax region of the decoy with his forelegs as other thynnines do on *Chiloglottis*, *Arthrochilus*, *Drakaea*, *Caladenia barbarossa*, and others.

Whereas some forms of *Caleana minor* are adapted for insect pollination others are apomictic (Jones 1977). In the Grampian Ranges of Victoria the apomictic forms all exhibit various kinds of deformities including immobile labellums, reduced or absent anthers and stigmas, and tightly bound pollinia that cannot be removed. Despite the non-functional anthers and stigmas, the plants develop viable seed capsules, with the swelling often beginning in the bud. These observations indicating apomixis were evaluated in potted plants by removing anthers from the buds of normal and deformed flowers (Jones 1977). Capsules developed only on the deformed plants, confirming apomixis. Similarly deformed plants known from the Blue Mountains of New South Wales are also likely to be apomictic (Jones 1977).

However, Bates (1983*a*) found that apomixis also occurred in *C. minor* of normal appearance in South Australia, though the data are limited. Only about 10 % of flowers in the study population had their pollinia removed, and no stigmas received pollen, yet all developed capsules with seed of normal appearance. This peculiar observation indicates *C. minor* has a mixed mating system. This has been confirmed by M. A. Clements (unpublished), whose embryological studies found that apomictic bodies are already present in the early stages of development and that capsules contain both fertilized and apomictic seed. Bates and Weber (1990) stated that all populations of *C. minor* examined in South Australia appear to be apomictic. Populations of *C. minor* in central eastern New South Wales may be similar to those in South Australia; flowers sexually attract thynnine wasp pollinators, which normally result in relatively low pollination percentages, yet all flowers develop capsules (C. Bower, unpublished). Further work is needed to assess the relationship between entomogamous outcrossing and apomixis in populations of *C. minor* throughout its range. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Species of *Caleana* are difficult to maintain in cultivation. **(HR)**

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39. CHILOGLOTTIS

Chiloglottis R.Br., *Prodr.*, 322 (1810). Type species: *Chiloglottis diphylla* R.Br.

Derivation of name

From the Greek *cheilos*, lip, and *glottis*, mouth of the windpipe, referring to the resemblance of the labellum and its callus to the human windpipe. **(DJ)**

Description (Plates 45–48; Fig. 39.1)

Perennial geophytic *herbs*. *Roots* filamentous. *Tubers* ovoid, solitary, fleshy, naked; replacement tubers absent; daughter tubers formed on the end of slender root-like stolons. *Stem* erect, short, unbranched, with membranous cataphylls at each node. *Leaves* two, basal, subequal, petiolate; lamina mostly elliptic, convolute in bud, margins entire; venation anastomosing; petiole grooved adaxially. *Inflorescence* single-flowered, erect, terminal; scape fleshy, with one sterile bract; floral bracts foliaceous, sheathing. *Flowers* resupinate, dull-coloured, pedicellate. *Dorsal sepal* free, much broader than the lateral sepals, incurved over the column, with or without a short terminal osmophore. *Lateral sepals* united at the base, with short to

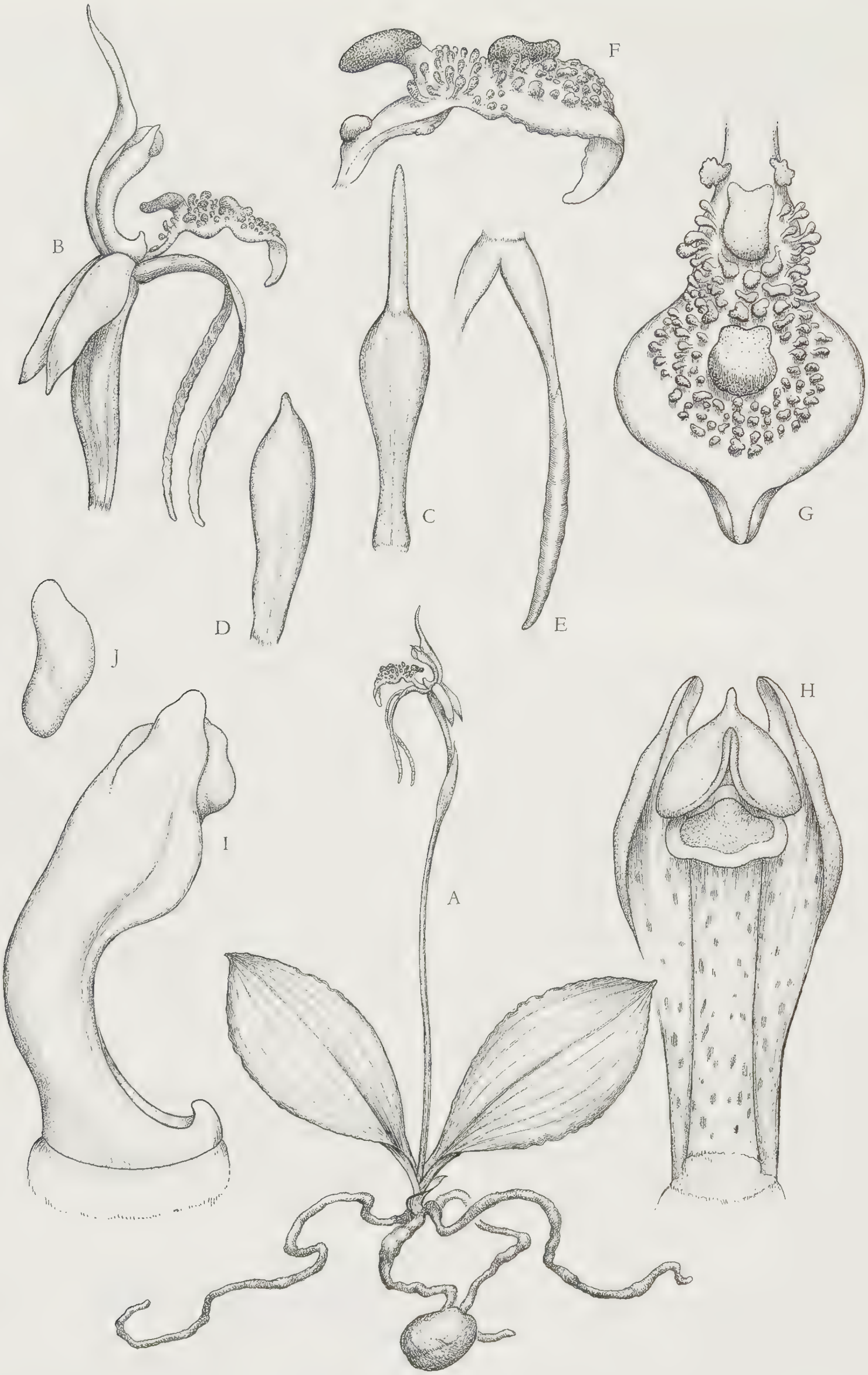

Fig. 39.1. *Chiloglottis longiclavata* D. L. Jones. A. Habit, ×1; B. Flower from side, ×3; C. Dorsal sepal, ×6; D. Petal, ×6; E. Lateral sepal, ×4.5; F. Labellum from side, ×9; G. Labellum from above, ×9' H. Column from front, ×12; I. Column from side, ×12; J. Pollinium, ×9. Drawn by Oliver Q. Whalley.

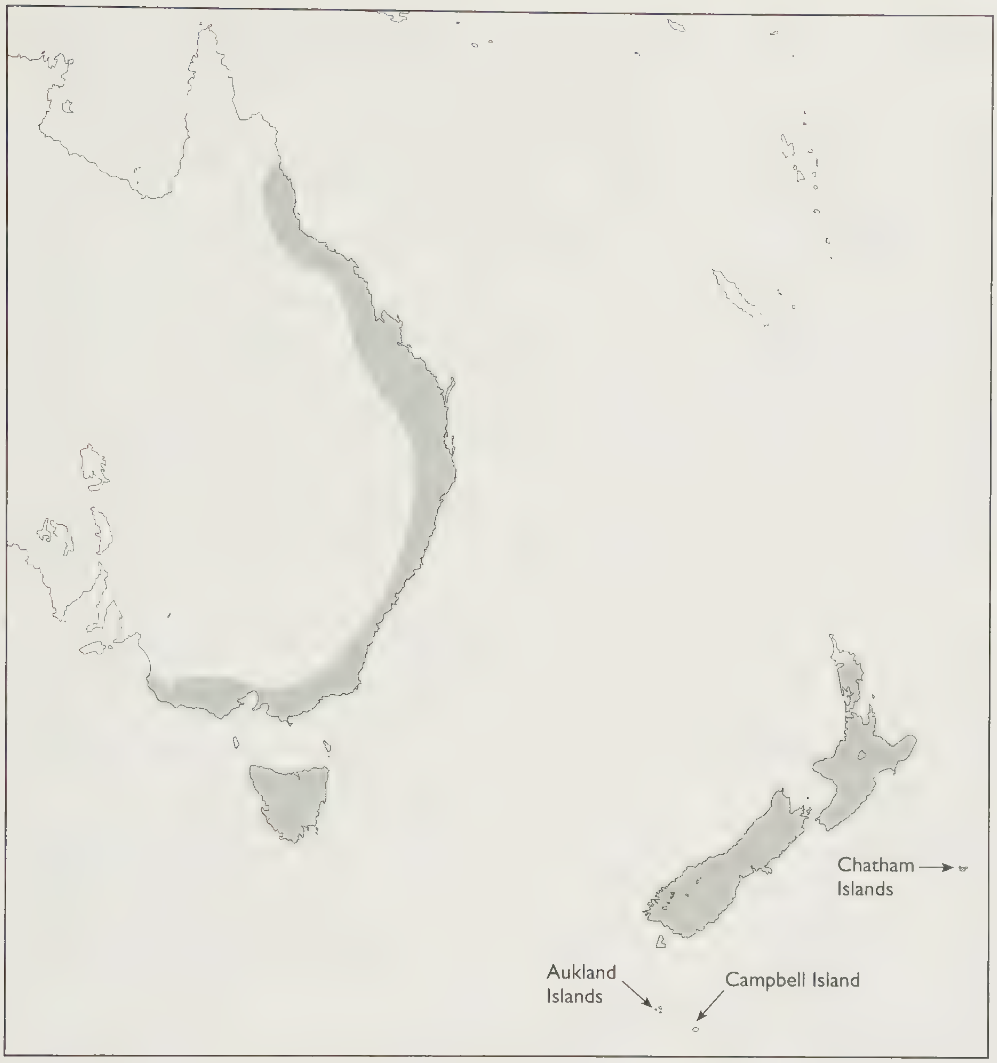

Fig. 39.2. Distribution map of *Chiloglottis*.

long terete terminal osmophores. *Petals* free, broader than the lateral sepals. *Labellum* free, attached by a small claw to the underside of the column foot, either of limited movement or tremulous, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina not lobed, either more or less cordate or rhombic-trapeziform; callus variable, consisting of calli in various shapes and sizes either in a strongly insectiform arrangement, in rows or clusters or more irregularly arranged; nectar absent. *Column* elongate, incurved, narrowly to broadly winged; column foot reduced to a vestigial bump; anther terminal, four-celled, persistent, basifixed, erect, rostrate; pollinia four, curved, flat, mealy, naked, yellow; rostellum ventral; stigma entire, circular, concave. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, glabrous, erect; sepals and petals persistent; pedicel considerably elongated and thickened in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 39.2)

A genus of about 27 species endemic in eastern Australia with two species in New Zealand and an additional widely distributed species occurring in Australia, New Zealand, Stewart Island, Chatham Island, and Campbell Island. **(DJ)**

Palynology

Tetrads of *C. gunnii* Lindl. are tetrahedral, *c.* 30 μm; inaperturate; tectate-imperforate distally, tectate-perforate along margins; psilate distally but fossulate to foveolate marginally, and supra-scabrate; the units globose-spherical (Ackerman and Williams 1981). **(AP)**

Ecology

Latitudinally in Australia *Chiloglottis* is distributed from about 17°16′ south on the Atherton Tableland, Queensland, to about 43° south in southern Tasmania. In New Zealand it is distributed from about 35° south in the North Island to about 52° south on Campbell Island. Species occur from near sea level to about 2000 m in the Snowy Mountains of south-eastern Australia. Species of *Chiloglottis* are terrestrial, although in southern Australia *C. cornuta* Hook.f. and *C. reflexa* Druce may occasionally colonize the fibrous trunks of the tree fern *Dicksonia antarctica*. Reproduction is by seed, and all species grow in clonal colonies that result from the production of daughter tubers on the end of root-like stolons. They occur in areas with a seasonal climate, and the plants have periods of active growth and dormancy. Two distinct flowering periods occur, with one group of species flowering in late summer and autumn and the others in spring and early summer. In the autumn-flowering species the buds emerge along with the leaves, but in the spring-flowering species the leaves are well developed before flowering takes place. Seed dispersal begins 8–12 weeks after pollination.

The greatest diversity within *Chiloglottis* occurs in south-eastern Australia in open forest, woodland, heathy forest, and heathland. In upland, montane, and subalpine regions plants also extend to moist grassy sites, boggy areas, and *Sphagnum* mounds. In New Zealand *C. cornuta* occurs in moist areas in forests, shrublands and grasslands and is also a frequent component in plantations of *Pinus* and *Eucalyptus* species. It is also recorded as being a frequent colonizer of mossy logs. **(DJ)**

Pollination

Chiloglottis is one of the better-studied genera of Drakaeiinae with regard to pollination. The results of many scientific studies indicate that all but one of the 30 or so species of *Chiloglottis* are pollinated by sexually deceived, male thynnine wasps. The exception is the autogamous *C. cornuta*.

The first observations of pollination by pseudocopulation in *Chiloglottis* were published by Dockrill (1956). He reported pollination of *C. formicifera* Fitzg., probably the subsequently described *C. platyptera* D. L. Jones (Jones 1991), by multiple pseudocopulating male 'ichneumons' in which several males piggyback each other while struggling for access to the pseudofemale. The third male in the pile reached the anther, removed the pollinia with its head, and then pollinated a second flower on top of another male. Subsequent work has shown this is not the normal mode of pollination in *Chiloglottis*, which is generally mediated by single males. Nevertheless, there are circumstances in which these extraordinary events could occur.

Giles (1964) reported a chance observation of wasps that attempted pseudocopulation on the labella of several flowers of *Chiloglottis reflexa*. A captured male bearing pollinia on its thorax was identified as a thynnine wasp.

Stoutamire (1974*a*, 1975, 1981) carried out the first systematic studies and is usually credited with being the first to recognize that *Chiloglottis* species are pollinated by sexual deceit and that male thynnine wasps are the exclusive vectors. He also outlined the key characteristics of the system. Males are attracted to flowers from a distance by odours mimicking the sex pheromones normally emitted by receptive females. Stoutamire (1975) found the odours emanated from dark maroon to black glands on the labellum, which may also function as visual mimics of the female. Pollination occurred when the males attempted to mate with the labellum.

The two main morphological types within *Chiloglottis* exhibit quite different pollination mechanisms. The small-flowered species in the *C. reflexa* group bear flowers above the ground on a peduncle 2–15 cm high. The large-flowered forms in the *C. gunnii* complex tend to have sessile or shortly pedunculate flowers near ground level. Labellum function varies between the two groups. In the small-flowered species the labellum is more or less rigidly attached to the base of the column and is passively mobile, but it can be overbalanced against the column in the large-flowered taxa.

Complex clusters of labellum calli mimic the shape of the ant-like female thynnine in *C. reflexa* group species. In some the mimicry is remarkably faithful to the original, such that *C. formicifera* was named by Fitzgerald (1877) for the ant-like appearance of its labellum calli. The head and thorax regions of the pseudofemale are represented by the major proximal stalked gland (Jones 1991). Behind this, the major sessile gland corresponds to the shiny abdomen along with aggregations of smaller sessile glands toward the labellum apex. The pseudofemale faces the column base with head and thorax below the overarching stigma and anther.

Correct alignment of males below the column is achieved by the positioning of the major proximal stalked gland. Attracted males grasp this gland just behind its thickened apex with their forelegs (Plate 46) as they would a female. They then probe with the abdomen around the labellum margins or among the apical calli in an attempt to couple prior to nuptial flight. While probing, the genital apparatus is expanded, and the wasp may rotate around the pseudohead region of the decoy. Some males may attempt to fly off with the decoy, lifting the labellum a little toward the column (Logan 1984; C. Bower, unpublished). These movements bring the thorax and any pollinia it may be carrying into contact with the stigma, if the wasp is large enough and the labellum has not begun to sag with age (C. Bower, unpublished). Departing wasps remove pollinia from the anther if the thorax is pulled past the rostellum and anther toward the labellum apex. The rostellum imparts a coating of glue (C. Bower, unpublished), which adheres to the pollinia as the one-way anther flaps are pushed aside. Because the labellum is open for wasps to enter and depart from many angles, not all visitors collect pollinia before leaving (C. Bower, unpublished), making these flowers seem mechanically inefficient.

The flowers of the *C. gunnii* complex function quite differently. The much larger labellum with upturned sides is passively mobile, and the glandular calli do not form an insectiform cluster. In most species there is a tall, stalked gland situated in the centre of the labellum lamina at the base, which is flanked by similar but shorter glands on either side. About two thirds of the way to the labellum apex is a short, broad, central gland. Two rows of calli of various sizes converge on the short apical gland from the basal lateral calli. The large central basal gland is the most important for pollination. It is functionally, and possibly morphologically, homologous to the major proximal stalked gland of the *C. reflexa* group. However, rather than facing toward the column as in *C. reflexa* it is angled away.

Male thynnines attracted to *C. gunnii* group flowers land on or near them and crawl to the labellum calli, which they appear to inspect. They quickly mount the central basal callus, grasping it with their forelegs just below the slightly expanded tip (Plate 47). This usually causes the labellum to collapse against the column enclosing the insect between the labellum and the hooded dorsal sepal (C. Bower, unpublished). This action presses the wasp's thorax against the stigma, effecting pollination if it is carrying pollinia. The wasp escapes by clambering forward over the central basal callus, where its thorax is forced past the rostellum to receive a coating of rostellar secretion and then picks up the pollinia from below the anther flaps (Plate 48). The *C. gunnii* group of *Chiloglottis* are the only thynnine-pollinated orchids in which the wasp picks up the pollinia while moving forward out of the flower; in all other taxa it occurs as they back out. Pollinia removal and pollination may also occasionally occur without labellum tipping when wasps clamber over the central basal callus while attempting to couple with the labellum margin in a manner similar to pollination in the *C. reflexa* group (Stoutamire 1974*a*; C. Bower, unpublished).

The sources of pseudo sex-pheromones that attract males to flowers are thought to be the labellum calli and/or collections of osmophores on the lateral sepals referred to as clubs. Stoutamire (1974*a*) showed that males of a species of *Eirone* were attracted to excised labellum calli of *C. gunnii s.l.* (probably *C. grammata* G. W. Carr; C. Bower, unpublished). In general, *C. gunnii* group species have small sepal clubs, and their role in the attraction of pollinators has not been evaluated.

By contrast, the small-flowered *C. reflexa* group species tend to have prominent clubbing. Peakall and Handel (1993) argued that male *Neozeleboria proxima* were attracted from a distance by odours emitted by osmophores on the lateral sepals of *C. trilabra* Fitzg. and that the labellum provided a short-range visual and tactile mimic of the flightless female. Field choice tests have shown that the lateral sepals and labellum of *C. trilabra* are equally attractive to male *N. proxima* but that males frequently attempt to mate with isolated labella and only rarely with the sepals (C. Bower, unpublished). Male *N. proxima* will sometimes grasp the sepals of whole *C. trilabra* flowers in the field and attempt to fly away with them (C. Bower, unpublished). It appears that the close-range visual and chemical mimicry of the labellum will occasionally be missed by incoming males.

Stoutamire (1975, 1981) noted that some *Chiloglottis* species appeared to attract only a single thynnine species but that *C. gunnii s. l.* in Tasmania attracted three different species as pollinators. However, each pollinator was attracted to morphologically distinct races within *C. gunnii*. He suggested that the races were reproductively isolated and may require taxonomic recognition, which has since been performed (Carr 1991; Clements 1993; Jones 1998*c*). Bower (1992, 1993, 1994, 1995, 1996*a*, *b*, 1997) conducted a large number of field pollinator-choice experiments to determine the degree of pollinator specificity among *Chiloglottis* species. These showed conclusively that within its normal geographical range and habitats each *Chiloglottis* species has only a single thynnine species as its pollinator. However, there are usually also one or more 'minor responders' that are attracted to the vicinity of the orchid flower but do not undergo the full sequence of behaviours needed to effect pollination. It is postulated that the orchid kairomone has sufficient resemblance to the pheromone of the minor responders to excite some curiosity but fails to stimulate pseudocopulation, in contrast to the pollinator for which the resemblance is likely to be more complete.

No cross-attraction of pollinators was found among sympatric *Chiloglottis* species (Bower 1993, 1994, 1995, 1996*a*, *b*). This high degree of pollinator specificity appears to be necessary to prevent introgression and maintain species integrity. Limited studies of interspecific genetic compatibility in *Chiloglottis* indicated that there are no significant post-zygotic barriers to hybridization (Peakall *et al.* 1997). However, some *Chiloglottis* species, when transported out of their normal ranges and habitats, may strongly attract and be pollinated by thynnines that are not their normal pollinators. An example is *C. seminuda* D. L. Jones, which is pollinated exclusively by *Neozeleboria* sp. 29 in its normal coastal sandstone habitats but may be pollinated by *Asthenothynnus westwoodi* when transferred to inland localities (Bower 1996*b*). Data such as these indicate that allopatric thynnine species may share nearly identical pheromones.

Cross-attraction of pollinators among allopatric *Chiloglottis* species may often occur (Bower 1994, 1995, 1996*a*). These may be one-way or two-way cross-attractions. For example, *C. pluricallata* D. L. Jones *s. str.* from the northern tablelands of New South Wales attracts and is pollinated by the pollinator (*Neozeleboria monticola*) of *C. valida* when transported to the southern tablelands of New South Wales, but the reverse does not occur when *C. valida* is transported to the northern tablelands. In contrast, *Chiloglottis* aff. *pluricallata* from the northern tablelands of New South Wales and *C. valida* D. L. Jones from the central and southern tablelands strongly attract and are pollinated by each other's pollinators, *Neozeleboria tabulata* and *N. monticola*, respectively.

Carefully designed pollinator-choice tests can be used in the field to distinguish closely related cryptic or sibling species of *Chiloglottis* on the basis of their pollinator specificity and inferred reproductive isolation (Bower 1994, 1995, 1996*a*, *b*). Several examples of sympatric and allopatric sibling species have been discovered in this way. *Chiloglottis pluricallata* on the northern tablelands of New South Wales comprises three cryptic species. *Chiloglottis pluricallata s. str.* is widespread in montane forests but coexists with two rare localized wet habitat taxa, one at each of Barrington Tops and Point Lookout. None of the three taxa attracts the pollinators of the others. Similarly, two morphologically almost identical but allopatric taxa that do not attract each other's pollinators occur within *C. palachila* D. L. Jones & M. A. Clem. one on the northern and the other on the central tablelands of New South Wales.

Similar field choice studies can be used to distinguish cryptic species among the thynnine pollinators of *Chiloglottis* on the basis of their responses to orchids (Bower and Brown 1997). This requires a greater number of studies at more localities than are needed to distinguish the orchids on the basis of their pollinators if the pollinators are not from complexes of cryptic species. Complexes of cryptic species have been uncovered in the *Neozeleboria monticola s.l.* pollinators of several species in the *C. valida* complex and in the *N. proxima* group, which pollinates several *C. reflexa* group species.

Only one natural hybrid has been documented in *Chiloglottis*, *C.* × *pescottiana* R. S. Rogers (Logan 1984; Peakall *et al.* 1997). The relative lack of recorded natural hybrids attests to the high degree of reproductive isolation in *Chiloglottis*. The parents of *C.* × *pescottiana* are *C. valida* and *C. trapeziformis* Fitzg., an unlikely combination as they are from two of the most morphologically different groups in the genus; the large-flowered, short *C. gunnii* group and the small-flowered, tall *C. formicifera* group, respectively. Morphometric analysis has shown that *C.* × *pescottiana* displays intermediate morphology between the two parents, and genetic analyses using enzyme electrophoresis have verified its parentage (Peakall *et al.* 1997). F_2 backcrossed plants are rare in the field, indicating that there is no hybrid swarm formation and little introgression. Artificial crosses showed that this may be partly due to lower pollen viability in *C.* × *pescottiana* and smaller F_2 seed, which may also be less viable.

Hybridization resulting in the formation of *C.* × *pescottiana* is due to the occasional overlap in distribution of *C. valida* and *C. trapeziformis*, which normally occur in different habitats (Bower *et al.*, unpublished). In general, *C. valida* occupies moist, montane forests, whereas *C. trapeziformis* mainly occurs in drier, low-elevation forests. The two orchids have different pollinators, *Neozeleboria cryptoides* for *C. trapeziformis* and *N. monticola* for *C. valida*. However, there is two-way cross-attraction by the orchids for the pollinators; *N. cryptoides* is able to remove the pollinia of both orchids in field tests. Field observations showed that both pollinators were less responsive to foreign species. Although pollinia removal from *C.* × *pescottiana* has been observed (Logan 1984), the intermediate morphology of the flowers between those of the two major types in the genus indicates its flower structure may not be mechanically optimal (Bower *et al.*, in manuscript).

A curious phenomenon exhibited by *Chiloglottis* species is the doubling in length of the flower pedicel after fertilization. This is usually interpreted as an adaptation to assist the dispersal of seed by wind (Jones 1988). Handel and Peakall (1993) and Peakall and Handel (1993) sought explanations for the selection of low floral height in *Chiloglottis* species by examining the responses of pollinators to flowers placed artificially at a range of heights among pollinator populations in the field. They concluded that the *Neozeleboria* pollinators of *C. reflexa* and *C. trilabra* search for females in a limited height range close to the ground. Flowers of *C. trilabra* grow from 6–17 (mean 12.3) cm high and elongate after fertilization to a mean of 24.2 cm. However, *Neozeleboria proxima*, the pollinator of *C. trilabra*, preferred flowers at heights of 15 and 22 cm above the ground but did not discriminate between them. Heights of 2–8 cm and 30–100 cm were less preferred. Contrary to expectation *N. proxima* did not discriminate between heights within the range of the tallest flowers and the seed capsules, and the lower flower heights were less preferred. There is no satisfactory explanation for this apparent anomaly.

Obligate autogamy occurs only in *C. cornuta* (Thomson 1879; Jones 1988; Molloy 1990; Stoutamire 1981). The mechanism of self-pollination is simple; the anther flaps curl back, allowing the coherent pollinia to fall from the anther onto the stigma below (C. Bower, unpublished). Facultative autogamy has been observed in *C. valida* in New Zealand (Molloy and Johns 1983) and Australia (Peakall *et al.* 1997). In both cases only a small proportion of individuals self-pollinated, and it seems clear that the dominant reproductive mechanism in *C. valida* is sexual deception. However, *C. valida* is a rare immigrant in New Zealand, and the thynnine pollinator is absent (Molloy and Johns 1983; Molloy 1990; G. R. Brown, unpublished). The lack of a pollinator may provide a selective advantage for autogamous individuals, leading eventually to obligate autogamy as in the case of *C. cornuta*. The long-term survival of *C. valida* in New Zealand may depend on both vegetative reproduction through tuber multiplication and development of autogamy. **(CCB)**

Uses

Species of *Chiloglottis* are cultivated by specialist growers. **(DJ)**

Cultivation

Most *Chiloglottis* species respond well in cultivation. There are species in flower throughout the year. The *C. valida* group are the most difficult to grow well. They do not appear above ground until winter, and in late spring they have to be keep damp over summer while their new tubers form. They need a well-drained mix or the tubers will rot.

Mix: basic or a little coarser for good drainage. Light: 50% shade. Watering: water while plants are in active growth, which for some species is almost 12 months of the year. Flowering: most *Chiloglottis* species flower freely. Those that flower in the early autumn, e.g. *C. reflexa*, are the least reliable. Propagation: most multiply well in cultivation, on average × 2. **(HR)**

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40. DRAKAEA

Drakaea Lindl., *Edward's Bot. Reg.* 1–23: *Swan Riv. Append.*, lv (1840). Type species: *Drakaea elastica* Lindl.

Drakaea Lindl. sect. *Eu-Drakaea* Schltr., *Bot. Jahrb. Syst.*, **45**, 383 (1911).

Derivation of name

Honouring Miss Sarah Anne Drake (1803–57), who prepared many illustrations for John Lindley's *Sertum Orchidaceum*, *Edward's Botanical Register*, and other publications. **(DJ)**

Description (Plates 49, 50; Fig. 40.1)

Perennial geophytic *herbs*. *Roots* filamentous. *Tubers* ovoid, solitary, fleshy, naked; replacement tubers formed on the end of short droppers; daughter tubers formed on the end of root-like stolons. *Stem* erect, short, unbranched, with membranous cataphylls at each node. *Leaf* one, basal, petiolate; lamina thick and spongy, mostly broadly ovate to orbicular, papillate, convolute in bud, margins entire; venation anastomosing; petiole short, deeply grooved adaxially. *Inflorescence* single-flowered, erect, terminal; scape wiry, with one small sterile bract, thin at the base, thickened distally; floral bracts reduced, sheathing. *Flowers* resupinate, dull-coloured, pedicellate. *Perianth* and column recurved, with the labellum projecting, insectiform. *Dorsal sepal* free, similar to the lateral sepals, recurved. *Lateral sepals* mostly free, the anterior base decurrent on the column foot. *Petals* free, subsimilar to the sepals. *Labellum* free, hinged to the apex of the column foot by a short claw, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina not lobed, variously folded and curved to resemble the body of an insect, peltately attached to a rod-like basal stalk; callus mostly terminal on the lamina, consisting of aggregations of shiny round or wart-like calli and ciliate clavate trichomes, the calli and trichomes also variously distributed on the lamina and labellum stalk; nectar absent. *Column* elongate, strongly recurved, often expanded or thickened toward the base; column wings fused to the column, often undulate, with an elongate, porrect projection toward the base; column foot nearly as long as the column; anther terminal, four-celled, persistent, basifixed, erect; pollinia four, curved, flat, mealy, naked, yellow; rostellum ventral; stigma entire, circular, concave. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, glabrous, erect; sepals and petals persistent; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 40.2)

A genus of about nine species endemic in south-west Western Australia. **(DJ)**

Palynology

Tetrads of *D. glyptodon* are rhomboidal, *c.* 42 μm; inaperturate; tectate-perforate; fossulate-scabrate; the units irregularly shaped (Ackerman and Williams 1981). **(AP)**

Ecology

Drakaea, which is endemic in south-western Western Australia, occurs between about 27° south and 35° south. Some species grow in low-lying areas that may be damp to wet in winter, whereas others favour well-drained sites. They often colonize disturbed sites such as tracks and embankments. Habitats include shrubland, *Kunzea* (Myrtaceae) thickets, woodland dominated by *Banksia* spp. (Proteaceae) or jarrah forest, heathland, and granite outcrops.

All species are terrestrial, reproducing from seed and also forming local sparse colonies by the formation of daughter tubers on the end of relatively long, thin root-like stolons. The plants occur in areas with a strongly seasonal climate. The leaf emerges above ground in late autumn and winter and is fully developed before flowering in spring. Seeds begin to be dispersed 8–12 weeks after pollination. **(DJ)**

Pollination

Like all other genera in Drakaeinae, *Drakaea* is adapted for pollination by sexual deception of male thynnine wasps (Stoutamire 1974*a*, 1975, 1981; Peakall 1990), similar to that of *Arthrochilus* and *Spiculaea*. The labellum consists of a physical and chemical mimic of a specific thynnine female (Plate 50). It is held away from the column on a long stalk-like foot that has a flexible hinge that can be rotated passively in a 180° vertical arc. When released, the labellum springs back to its original position.

The head region of the insectiform decoy consists of a large warty dark-coloured callus facing the column. The callus usually has a narrower base representing the slender thoracic region of the female. The remainder of the labellum, representing the abdomen, is predominantly maroon in colour and adorned with clusters of hairs and small calli.

Stoutamire (1974*a*) described the behaviour of pollinators and the pollination mechanisms for *D. elastica* (now *D. livida* J. Drumm.) and *D. glyptodon*. Male *Zaspilothynnus nigripes*, the pollinator of *D. livida*, search for females low over the ground in patrolling flight. When they intersect the pseudo sex pheromone trail emitted by a flower they swoop back to regain the trail, then fly upwind in a zig-

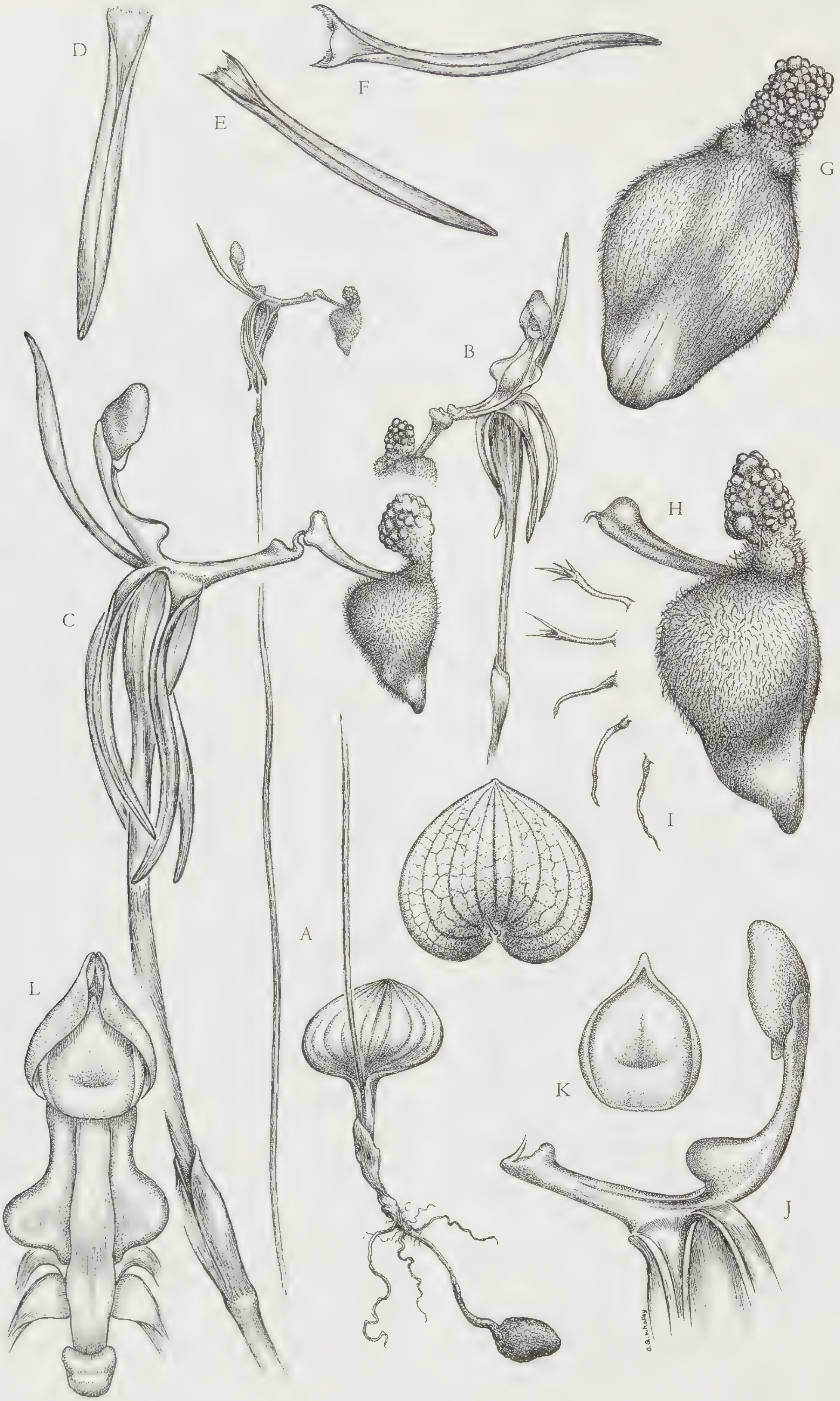

Fig. 40.1. *Drakaea glyptodon* Fitzg. A. Habit, ×0.9; B. Flower, oblique view, ×1.35; C. Flower with ovary and bract, ×4.05; D. Dorsal sepal, ×4.05; E. Petal, ×4.05; F. Lateral sepal, ×4.05; G. Labellum from above, ×5.4; H. Labellum from side, ×5.4; I. Basal hairs, labellum, ×54; J. Column from side, ×8.1; K. Stigma, ×8.1; L. Column from front, ×8.1. Drawn by Oliver Q. Whalley from Kew Spirit Collection nos. 33848 and 47037.

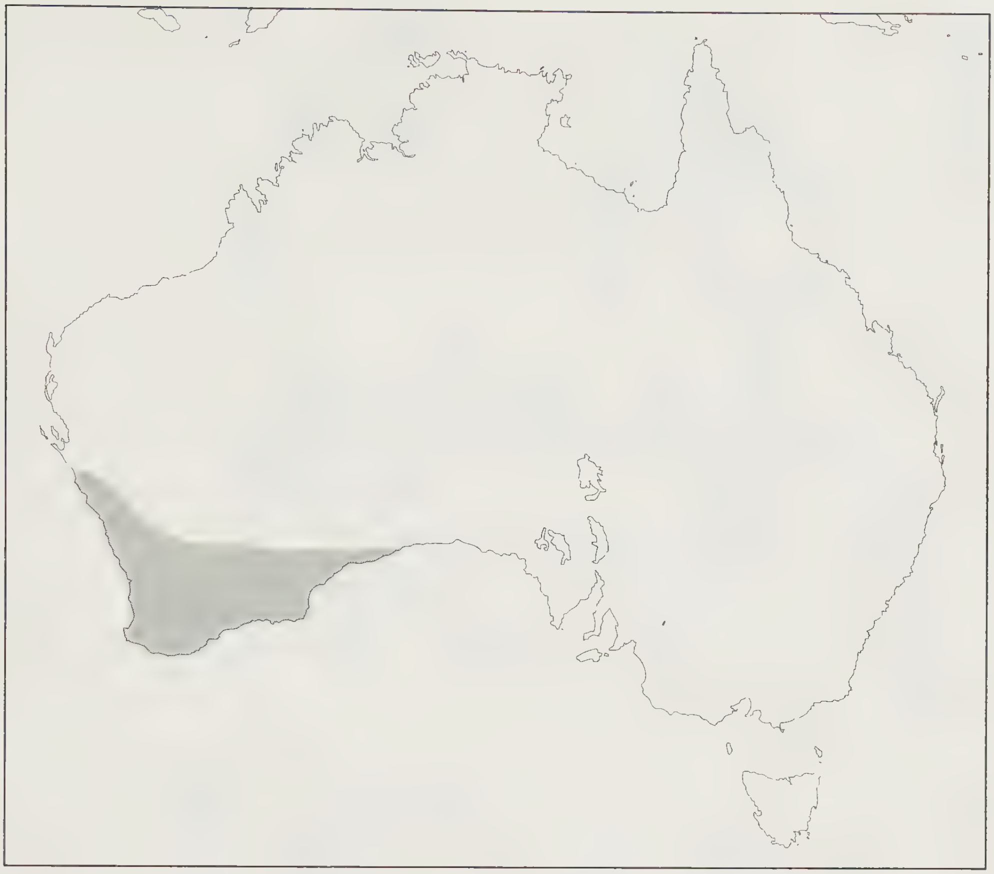

Fig. 40.2. Distribution map of *Drakaea.*

zag flight pattern to stay within it. The flight becomes more direct as the wasps close in and land on the labellum decoy. The wasp probes the sides and apex of the labellum with its curved abdomen before grasping the decoy and attempting to fly off. The precise orientation of the wasp on the labellum was not given by Stoutamire (1974*a*) or Peakall (1990), but the male probably seizes the thorax region of the decoy with his forelegs and holds the labellum margin with his other legs, as in *Arthrochilus* and *Chiloglottis.*

The attempted flight swings the hinged labellum and the wasp head-downward against the column, forcing the wasp's thorax into the stigma. This action spreads the friable pollen across the stigmatic surface if the wasp is carrying pollinia from a previous flower visit. To escape, the wasp struggles backward along the labellum, brushing its thorax past the rostellum where it receives a coating of glue. The sticky thorax then pushes the anther flaps apart, allowing contact with the pollinia, which are withdrawn. The labellum falls passively back to its resting position when the wasp departs. *Drakaea* flowers lack the prominent hooked column wings found in *Arthrochilus* and *Spiculaea* that help to orient and constrain the pollinator. This indicates that, as in *Chiloglottis*, the pollinator may be able to depart the decoy sideways as well as backward.

Peakall (1987, 1990) studied the comparative behaviour of male *Zaspilothynnus trilobatus* in response to its females and the orchid it pollinates, *D. glyptodon.* These studies provided a number of fundamental insights into the functioning of the thynnine pollination syndrome. Peakall (1990) found there was intense competition among male *Z. trilobatus* for females and suggested that this may be critical for pollination success in *Drakaea.* Most receptive females (61%) were located and picked up by males within one minute of their presence, and all were carried off within five minutes. Several males often approached the female at about the same time with the first to arrive usually flying off with her in copula (73% of cases).

Experiments with hidden live females to provide the long-range chemical attraction and nearby (2–3 cm) exposed dead females as visual cues showed that 98% (n = 295) of attracted males failed to land on the decoy, and only 1.2% attempted to carry it away (Peakall 1990). Thus the sources of visual and chemical stimuli must coincide for the consummation of mating behaviour in *Z. trilobatus.* This condition is met in *Drakaea* species that lack the osmophores found on the sepals and petals in some other thynnine-pollinated genera such as *Caladenia* and *Chiloglottis.* Instead, all odours appear to emanate from the labellum in *Drakaea.*

Baiting trials with *D. glyptodon* flowers in an area where *Z. trilobatus* is abundant but the orchid is normally absent showed a similar rapid response by males to the introduction of flowers as for females. Most males arrived in the first minute, with the response tailing off over time. In trials lasting 15 minutes the mean number of wasps attracted in successive five-minute intervals was about 5.4, 2.3, and 1.2. These data, as well as mark–recapture experiments, indicate that males do not revisit flowers for at least 80 minutes after an initial encounter, a period Peakall (1990) termed the refractory response. Such a reaction to flower visits may account for the rarity of observations of pollinators on sexually deceptive species in the field. The refractory response implies a degree of learning ability by male thynnines (Peakall 1990), an attribute common to many Hymenoptera. It is not known whether males learn to avoid the location of stimuli or particular chemical signals.

A much lower proportion of *Z. trilobatus* males (21%) attempted to fly away with the *D. glyptodon* labellum in contrast to the response to live females (69%) (Peakall 1990), indicating that the labellum decoy is not convincing at close range to many wasps. However, of the males that flew away with the labellum decoy, 77% were thrown against the column. Comparative trials with five flowers at different stages of anthesis showed that attractiveness to male wasps varies among individuals. Peakall (1990) also found that the responses of different males to the same flower varied greatly. Some 7% of males broke off the approach without landing and were clearly not greatly excited. Although 93% landed, only 16% were stimulated to fly with the decoy. Peakall (1990) concluded that for pollination to occur the stimulus quality of the orchid must be high and/or the stimulus threshold of the wasp low. The role of learned avoidance of orchids in decreasing wasp responses over time remains to be determined.

There are several important consequences of the behaviours of male thynnines for the breeding system of *Drakaea* and other thynnine-pollinated orchids. The refractory period, during which the male wasp avoids particular orchid flowers, indicates the chances of self-pollination will be low. Males bearing pollinia will tend to visit flowers they have not previously encountered, thereby promoting outcrossing. It would appear that the chances of a flower being pollinated are highest when the flower first opens. At this time it is most highly attractive, and none of the local male pollinators will have encountered it. However, it is not known how long the refractory period lasts or whether wasps must revisit flowers to reinforce it.

Early accounts of sexual deception in the European genus *Ophrys* (Kullenberg 1961) and in the Australian *Cryptostylis* (Coleman 1927, 1928*a*) indicated that an essential attribute of hymenopteran pollinators was the naïveté of males, most of which emerge as adults before the females. It was believed that only males with no experience with true females could be duped by orchid decoys. Peakall (1990) showed that marked males visited orchids over a two-week period when females were abundant in the population. Pollination was clearly not restricted to a period when females were absent. In addition, males in at least some thynnine species do not always emerge earlier than females (Ridsdill Smith 1970). **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Species of *Drakaea* are difficult to maintain in cultivation. **(HR)**

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41. SPICULAEA

Spiculaea Lindl., *Edward's Bot. Reg.* 1–23: *Swan Riv. Append.*, lvi (1840). Type species: *Spiculaea ciliata* Lindl.

Derivation of name

The interpretation of the generic name *Spiculaea* is uncertain; it is derived from the Latin *spicula*, sharp point or sting, and may refer to the labellum that has the appearance of an insect with a large stinger. **(DJ)**

Description (Plate 51; Fig. 41.1)

Perennial geophytic *herbs*. *Roots* filamentous. *Tubers* ovoid, solitary, fleshy, naked; replacement tubers and daughter tubers formed on the end of short droppers. *Stem* erect, short, unbranched, with membranous cataphylls at each node. *Leaf* one, basal, petiolate; lamina firm to coriaceous, convolute in bud, purplish abaxially, margins entire; venation anastomosing; petiole grooved adaxially. *Inflorescence* racemose, few to many flowered, erect, terminal; scape wiry, with one sterile bract, thin at the base, thickened distally, withering upward as anthesis proceeds; floral bracts reduced, semi-sheathing. *Flowers* resupinate, dull-coloured, shortly pedicellate. *Dorsal sepal* free, slightly larger than the lateral sepals, incurved. *Lateral sepals* free. *Petals* free, much narrower than the sepals. *Labellum* free, hinged to the column foot by a short claw, appearing as an insectiform lure, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina much reduced, not lobed, with a rod-like peltate basal stalk; callus dominating the labellum, fleshy, ornamented with multicelled, clavate, ciliate trichomes; nectar absent. *Column* elongate column wings fused to the column, with two pairs of elongate, curved, unequal, wing-like projections, the larger one barbed, situated medially, the smaller one projecting beside the anther, often with an irregular dorsal lobe extending above the anther; column foot short; anther terminal, four-celled, persistent, basifixed, porrect; pollinia four, bilobed, flat, mealy, naked, yellow; rostellum ventral; stigma entire, circular, concave. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, glabrous, erect; sepals and petals persistent; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 41.2)

A monospecific genus endemic in south-west Western Australia. **(DJ)**

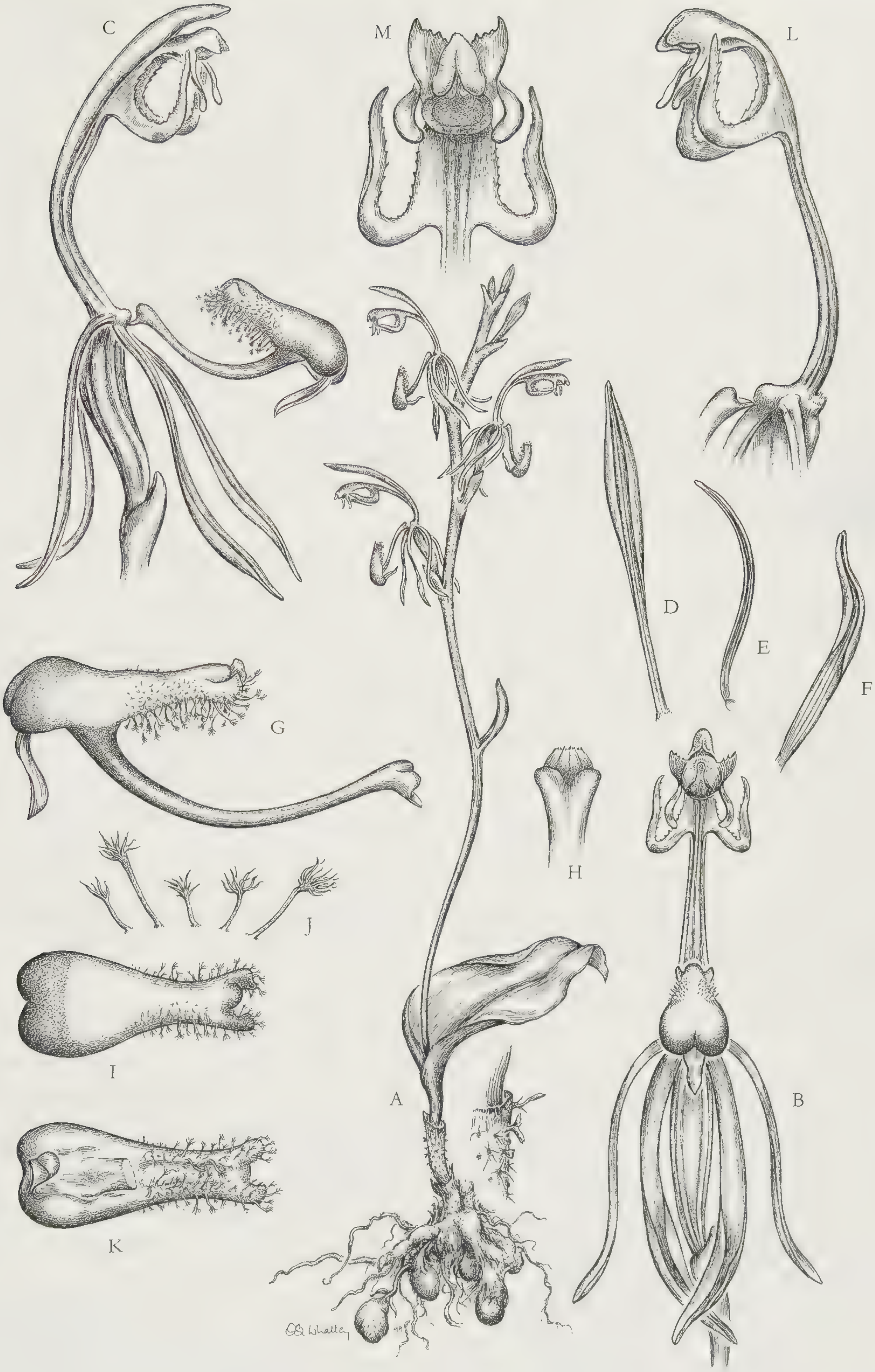

Fig. 41.1. *Spiculaea ciliata* Lindl. A. Habit, ×1 (note: leaf is withered at anthesis; see text); B. Flower from front, ×6; C. Flower from side, ×6; D. Dorsal sepal, ×6; E. Petal, ×6; F. Lateral sepal, ×6; G. Labellum from side, ×12; H. Labellum claw, ×12; I. Labellum from above, ×12; J. Labellum trichomes, ×45; K. Labellum from below, ×12; L. Column from side, ×9; M. Column from front. Drawn by Oliver Q. Whalley after W.H. Nicholls (1969) and from Kew Spirit Collection nos. 36097 and 33907.

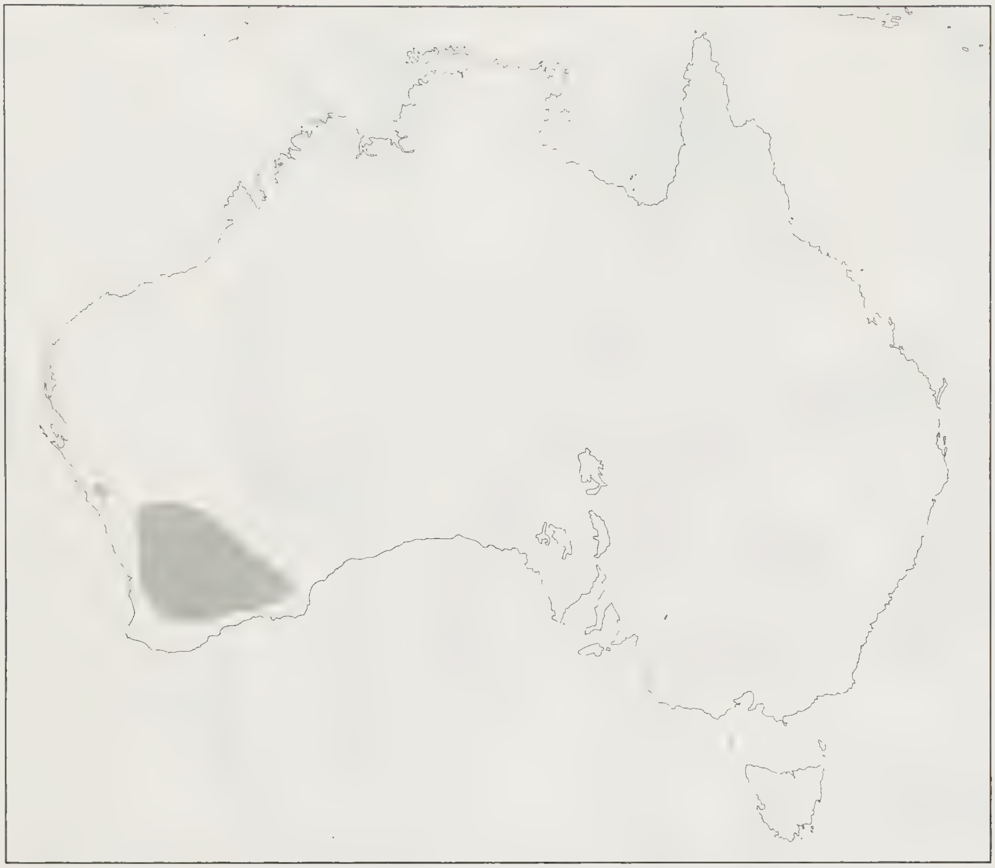

Fig. 41.2. Distribution map of *Spiculaea*.

Palynology

Monads of *Spiculaea ciliata* are globose-spherical and somewhat angled, 18–24 μm; monoaperturate, simple, tenuate-porate; tectate-perforate; and scabrate-fossulate (Ackerman and Williams 1981). **(AP)**

Ecology

Spiculaea ciliata, a remarkable orchid with bizarre flowers, is endemic in south-western Western Australia, with its main distribution between about 29° south and 33°40' south, and a small disjunct population near Kalbarri at about 27°40' south. It is confined almost exclusively to shallow sandy soils that overlay sheets and outcrops of granite, with the plants growing among moss and forbs, particularly cushions of *Borya* (Boryaceae). The prevailing climate is strongly seasonal with rain falling in autumn, winter, and early spring and the summers severely hot and dry. The leaf, which is fully developed prior to the emergence of the inflorescence, withers before the first flowers open in late October. The scape itself is fleshy and apparently contains sufficient nutrients and water for the flowers and capsules to develop during the heat of late spring and early summer. As successive flowers open the base of the scape withers upward, and much of it is dead by the time seed has been shed from the last capsule. The plants survive the formidable extremes of summer in their environment of shallow sandy soil over rock as dormant fleshy tubers. Reproduction is by seed. Clonal tufts are formed by the production of daughter tubers on the end of short droppers. Seeds begin to be dispersed 6–12 weeks after pollination. **(DJ)**

Pollination

Spiculaea ciliata appears to be pollinated exclusively by a single species of sexually deceived male thynnine wasp, an undescribed species of *Thynnoturneria* (Stoutamire 1985). As in other thynnine-pollinated genera, the labellum of *Spiculaea* comprises a physical and chemical mimic of the pollinator's female. The following account is based on Stoutamire (1985) but is expanded by the author (C. Bower, unpublished) in the light of current understanding of the thynnine pollination syndrome.

The labellum of *S. ciliata* consists of a long cylindrical arm with an insect-like structure attached at an angle of about 35° to its apical end. It is attached basally to the foot of the column via a loose hinge. At rest the labellum is below the column with the pseudofemale aligned in a head-up position as if clinging to a piece of dry grass. The upper part of the column is held over the labellum and features two pairs of slender column appendages. Two straight, prong-like wings project down on either side from a position between the adjacent anther and stigma. Opposing the prongs is a pair of hooked appendages positioned so that there is a small gap between the tips of the hooks and the bases of the prongs. The labellum decoy is situated between the two pairs of appendages when it is lifted against the column.

The decoy is not as persuasive an insect mimic to the human eye as those of some other Drakaeinae. Nevertheless, it has several features in common with other decoys that seem to be essential for stimulating and orienting thynnine pollinators. The 'head' region comprises dark-coloured glandular calli, and the tip of the 'abdomen' is covered in maroon callousing. These are probably the sources of the pseudopheromone odours. By dissecting the decoy and presenting different parts to pollinator populations in the field, Stoutamire (1985) found that the long-distance attractant was secreted only by the large maroon glands on the 'abdomen' of the decoy. Two lateral ear-like calli, which most likely represent the eyes of the female, broaden the head region. The narrower section behind the head of the decoy parallels the slender thorax of the female, which is grasped by the forelegs of the deceived male thereby orienting him correctly.

Attracted *Thynnoturneria* males fly upwind in a zig-zag path to the flower and land on or near the labellum. They grasp the decoy behind the head and attempt to fly away with it. This action lifts the labellum between the column appendages where the bases of the rapidly beating wings are guided along the prongs and around their curved base onto the hooks. Thus temporarily constrained, the male is in the correct position to deposit pollen if he is carrying pollinia on his thorax. As he struggles to free himself pollen is smeared over the stigma. To disengage from the hooks the wasp must move backward, probably by walking down the decoy, which he continues to hold. As he moves past the anther his thorax is coated in viscid secretion from the rostellum before pushing apart the anther flaps to contact and remove the pollinia. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Spiculaea ciliata, rarely seen in cultivation, requires a gravelly mix. Water when growing, but cease entirely over summer while the plants continue to flower. Propagate from seed, spread around parent plants. **(HR)**

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SUBTRIBE MEGASTYLIDINAE

Megastylidinae Schltr., *Notizbl. Bot. Gart. Berlin-Dahlem*, **9**, 570 (1926) (Megastylideae). Type: *Megastylis* (Schltr.) Schltr.

Description

Glabrous, tuberous or rhizomatous, geophytic *herbs*. *Tubers* elongate or globose, naked, rarely absent. *Leaf* solitary or rarely clustered, rarely absent, sessile or petiolate, convolute, flat or channelled, erect. *Inflorescence* single-flowered or racemose. *Flowers* resupinate, dull-coloured; tepals subsimilar. *Labellum* fixed to the base of the column; lamina unlobed or three-lobed, with irregular ridges, thickenings or calli; nectar present or absent. *Column* elongate; column foot absent or small; pollinarium present or absent; pollinia two or four. *Fruit* a dehiscent capsule. **(DJ)**

Anatomy

Leaf

SURFACE

Hairs absent, but papillae on both surfaces in *Pyrorchis*. Epidermis: cells rectangular to polygonal; walls thick with conspicuous pit-fields; anticlinal walls sinuous in *Pyrorchis*, *Rimacola*, and *Leporella*. Stomata restricted to abaxial surface, except on both surfaces in *Leporella* and *Pyrorchis* and on adaxial surface only in *Lyperanthus*.

TRANSECTION

Cuticle: thin (less than 3 μm), smooth to papillate. Epidermis: cells elliptical, isodiametric to polygonal, the outer wall often differentially thickened, especially at leaf margins. Stomata superficial, substomatal chambers shallow. Hypodermis absent. Mesophyll heterogeneous or homogeneous according to taxon. Palisade mesophyll in *Lyperanthus* unusually abaxial with the chloroplasts oriented in an adaxial arc in individual cells. Spongy mesophyll lacunar-stellate in *Leporella*. Vascular bundles as for the tribe. Xylem tracheary elements bibrachiate in *M. glandulosa* (Schltr.) Schltr. Largest vascular bundles in *M. gigas* (Rchb.f.) Schltr. and in *M. latilabris* (Schltr.) Schltr. hourglass-shaped. Sclerenchyma bundle caps present only as one row of fibres ad- and abaxially in *M. gigas*. Bundle-sheath cells thin-walled; 2–3 layered in *M. latilabris*. Bundle-sheath two-layered in *Rimacola*. Ergastic substances: raphides in unmodified chlorenchyma cells and/or mesophyll idioblasts in all but *Rimacola*. Inclusions of an unspecified nature, not birefringent in polarized light and often surrounded by a transparent sheath in many epidermal cells of *Burnettia* (bract only).

Collar/stem

TRANSECTION

Hairs on collar unicellular or multicellular, the multicellular type uniseriate in *Burnettia*, multiseriate in *Lyperanthus*, *Pyrorchis*, and

Rimacola, unbranched, associated with mycorrhiza; absent in *Megastylis* and *Leporella*. Cuticle thin, smooth to striate. Epidermis: cells rectangular, elliptical, to polygonal, the outer wall usually thickened; heavily sclerified in *Lyperanthus*. Stomata present or absent depending on taxon. Ground tissue parenchymatous, outer and middle layers of collar usually infected with hyphae and pelotons, the inner layers of stem sclerotic, forming a multilayered sclerenchyma sheath. Cell walls often provided with secondary suberized, banded thickenings. Several subepidermal layers in *Lyperanthus serratus* Lindl. heavily sclerified. Endodermis of collar: cells elliptical to polygonal with casparian strips. Vascular bundles collateral, often arranged in 1–2 rings with or without a few central bundles, the outer ring frequently abutting sclerenchyma sheath. Xylem tracheids primarily with helical or scalariform thickenings, although annular and pitted occur in some species. Crystals: raphides and/or rod-shaped crystals in cortex and/or ground tissue of most species.

Tuber

TRANSECTION

Hairs absent or present depending on taxon; if present, multiseriate, unbranched, associated with mycorrhiza. Velamen 1–3 layered, cells elliptical to polygonal and often periclinally compressed; walls suberized, of uniform thickness. Exodermis: cells elliptical to polygonal, walls of uniform thickness or thicker on outer and/or radial walls depending on species. Ground tissue parenchymatous; outer layers often infected with hyphae and pelotons, dissociated with age of tuber. Endodermis: cells elliptical to polygonal. Stele dissected or not depending on taxon; if dissected, 2–10 discrete vascular strands, each 1–13 arch and enclosed by endodermis; if undissected, medullated. Xylem tracheids mainly with scalariform or pitted thickenings. Ergastic substances: starch grains and raphides and/or rod-shaped crystals in ground tissue.

Root

TRANSECTION

Hairs unicellular, associated with mycorrhiza; absent in *Burnettia*. Velamen 1–2 (–4) layered, cells elliptical to polygonal; walls of uniform thickness or outer wall and/or radial walls of outermost layer thickened, depending on taxon. Exodermis: cells elliptical to polygonal, walls of uniform thickness. Cortex parenchymatous, occasionally infected with hyphae and pelotons, occasionally with starch grains. Endodermis: cells elliptical to polygonal. Stele medullated, 2–12 arch. Xylem tracheids with helical, scalariform, or pitted thickenings. Crystals: raphides or rod-shaped crystals in cortex. **(AP)**

Palynology

Nothing has been published about the pollen ultrastructure of Megastylidinae. **(AP)**

Phytochemistry

There are no phytochemical data recorded for Megastylidinae. **(NV, RG)**

Phylogenetics

Schlechter (1926) characterized this subtribe as belonging to tribe Polychondreae (= Neottieae) within Division Acrotonae by virtue of plant habit; regrowth from a short rhizome with fasciculated fleshy roots, usually fusiform; leaves basal, few, sub-coriaceous, fleshy, usually petiolate at the base; flowers medium or large in a several-flowered raceme; scape provided with distinct bracts, spurless labellum, mobile or sub-mobile; anther almost free at the back; and column with margins scarcely winged. He included only the genus *Megastylis* within this subtribe, placing the subtribe near Pachyplectreae (= Pachyplectroninae) and Chloraeeae (= Chloraeinae). Megastylidinae have, however, subsequently either been ignored or treated as part of the subtribe Chloraeinae (Dressler

Artificial key to the genera of Megastylidinae (DJ)

1. • Plants evergreen; rootstock with fleshy roots but lacking tubers 2
• Plants seasonally deciduous; rootstock with fleshy tubers 3

2. • Stems branched; labellum sessile; callus a basal plate with low parallel ridges . . . . .47. ***Rimacola***
• Stems unbranched; labellum clawed; callus with irregular rows of calli . . . . .45. ***Megastylis***

3. • Leaves absent from flowering plants; basal bract enlarged, leaf-like, reddish to purplish . . . . .42. ***Burnettia***
• Flowering plants bearing green leaves 4

4. • Leaves 1 or 2 per shoot; main leaf veins red; petals markedly dissimilar to lateral sepals; labellum lamina wider than long, hairy . . . . .43. ***Leporella***
• Leaf 1 per shoot; main leaf veins green; petals subsimilar to lateral sepals; labellum lamina longer than wide, glabrous 5

5. • Leaves petiolate on sterile plants and sessile on flowering plants; labellum clawed; labellum lamina undivided . . . . .48. ***Waireia***
• Leaves sessile on both sterile and fertile plants; labellum sessile; labellum lamina 3 lobed 6

6. • Leaf erect; leaf lamina much longer than wide, its margins incurved to involute; abaxial surface minutely papillate . .44. ***Lyperanthus***
• Leaf prostrate; leaf lamina about as wide as long, its margins flat; abaxial surface glabrous . . . . .46. ***Pyrorchis***

1981, 1993) based on the putative similarity of floral and pollen morphology (Ackerman and Williams 1981). Recent research on embryogenesis by Clements (1995) and the results of molecular analysis of the representatives of the Australasian and South American terrestrial genera (Clements *et al.*, in preparation) isolate the group from Chloraeinae, placing it within a broader Diurideae. Molecular analyses also cluster *Megastylis* within the Diurideae, along with five other genera hitherto treated as belonging to subtribe Caladeniinae. Results of these molecular analyses show that Megastylidinae are more closely related to Thelymitrinae and Drakaeinae than to Caladeniinae as was previously thought. Not all species of *Megastylis* fall into this clade in analysis of the plastid genes *rbcL* and *matK* (Kores *et al.* 1997, 2000); more research is needed to resolve this problematic situation. **(MAC)**

42. BURNETTIA

Burnettia Lindl., *Gen. Sp. Orchid. Pl.*, 517 (1840). Type species: *Burnettia cuneata* Lindl.

Derivation of name

Commemorating Gilbert T. Burnett, first Professor of Botany at Kings College, London. **(DJ)**

Description (Plate 52; Fig. 42.1)

Perennial geophytic monocarpic *herbs*. *Roots* filamentous. *Tubers* obovoid, solitary, fleshy; replacement tubers absent; daughter tubers absent. *Stem* erect, short, unbranched, with a membranous cataphyll at the apical node. *Leaves* absent. Basal bract usually one, foliaceous, sessile, sheathing, purplish, subcoriaceous, convolute in bud, glabrous, margins entire; venation weakly anastomosing. *Inflorescence* racemose, 1–few flowered, erect, terminal; scape with one or two loosely sheathing sterile bracts; floral bracts foliaceous, loosely sheathing. *Flowers* resupinate, dull-coloured, pedicellate. *Dorsal sepal* free, broader than the lateral sepals, cucullate over the column. *Lateral sepals* free. *Petals* free, subsimilar to the lateral sepals. *Labellum* free, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina membranaceous, three-lobed, the ventral surface papillate, margins entire, apex papillate; callus of two irregular central ridges or slender plates with variable blunt teeth on the proximal third of the lamina; nectar absent. *Column* elongate, slender, incurved, narrowly winged throughout; column foot absent; anther terminal, two-celled, persistent, basifixed, erect, rostrate; pollinia two, naked, granular, yellow; rostellum ventral, transverse; stigma entire, small, concave. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, glabrous, erect; perianth persistent; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 42.2)

A monospecific genus endemic in south-eastern Australia. **(DJ)**

Ecology

Burnettia cuneata Lindl. is a saprophyte that has an almost exclusive association with the myrtaceous shrub *Melaleuca squarrosa* Donn, which grows mainly in pure stands in dense lowland swamps and swampy thickets developed on wet peaty soils of low fertility. Less commonly both the orchid and its host occur in smaller soaks and localized seepage areas, sometimes even on sloping ground or near the tops of low hills. This species, which is primarily an orchid of the lowlands, has a fragmented distribution from the Blue Mountains, New South Wales (about 33°40′ south), to about 43° south in southern Tasmania.

Flowering of *Burnettia* occurs in spring and is primarily induced by hot summer fires. Massed floral displays over extensive areas can occur following such events. It is monocarpic, the plants dying after flowering. Replacement tubers are not produced, and the tubers of flowering plants are shrivelled at anthesis. In addition, sites containing marked flowering plants have revealed no evidence of the orchid when excavated one year later. Nothing is known about the germination or developmental phases of *Burnettia* prior to flowering. A few plants may flower in the second year after a fire. There has been at least one observation of flowering plants appearing some four years after a fire in Tasmania. Many questions remain about the life cycle of this species, and considerably more detailed research is needed. **(DJ)**

Pollination

There are no published reports of pollination in *Burnettia* except that Jones (1988) stated it is not self-pollinating. The close alignment of the labellum with the dorsal sepal to form a long vertical tube enclosing the column indicates the pollinators of *B. cuneata* are native bees that enter the tube seeking nectar. This is reinforced by the bright white radially arranged lateral sepals and petals typical of many bee-pollinated flowers (Faegri and van der Pijl 1979). There are no reports indicating whether nectar or odour is present. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

A leafless saprophyte, not amenable to cultivation. **(HR)**

Taxonomic literature

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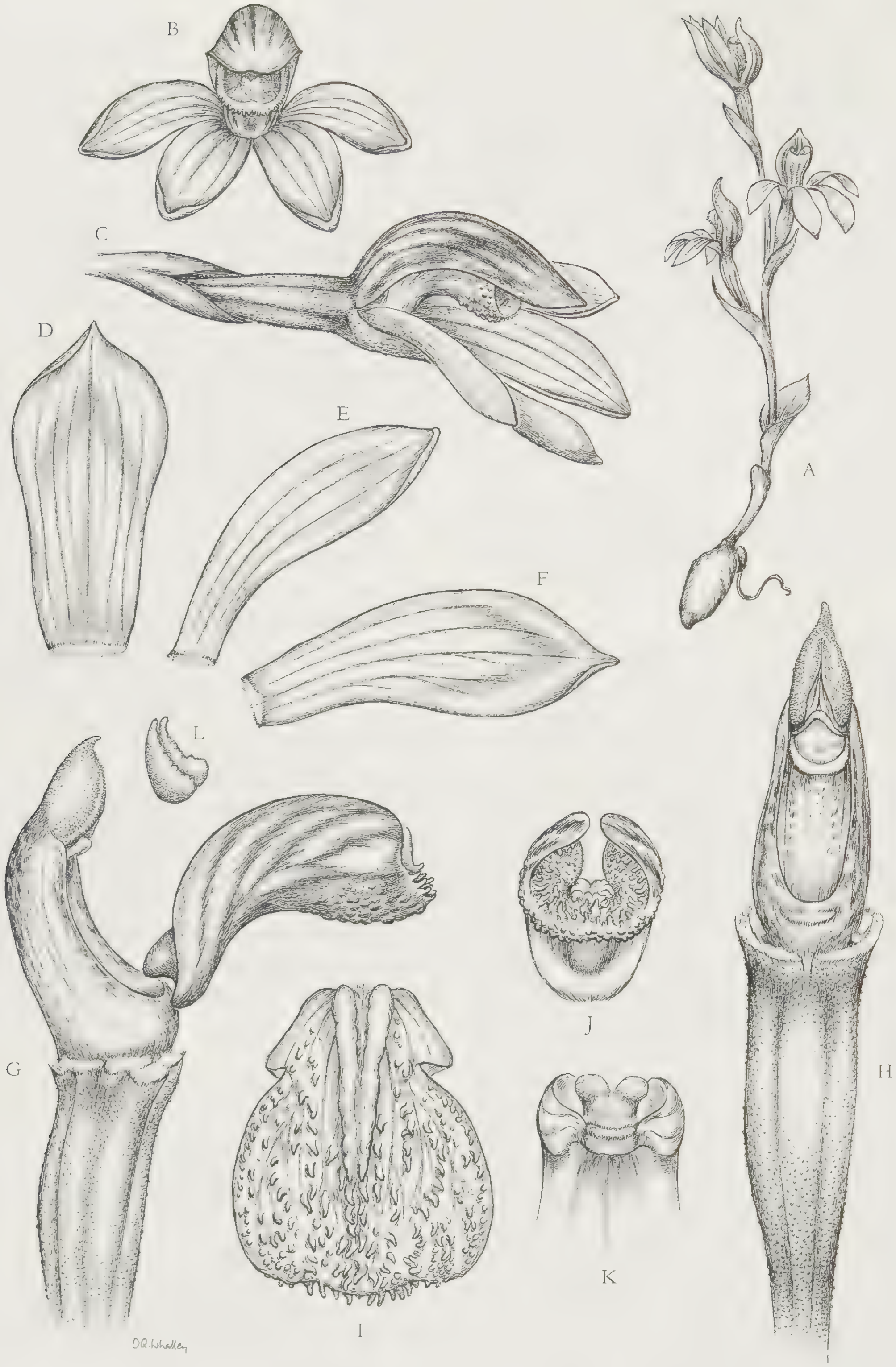

Fig. 42.1. *Burnettia cuneata* Lindl. A. Habit, ×0.9; B. Flower from front, ×2.7; C. Flower from side, ×2.7; D. Dorsal sepal, ×5.4; E. Petal, ×5.4; F. Lateral sepal, ×5.4; G. Labellum and column from side, ×8.1; H. Column from front, ×8.1; I. Labellum flattened, from above, ×8.1; J. Labellum apex, ×8.1; K. Labellum base showing callus, ×10.8; L. Pollinia after W. H. Nicholls (1969), ×8.1. Drawn by Oliver Q. Whalley from Kew Spirit Collection no. 53107.

Fig. 42.2. Distribution map of *Burnettia.*

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43. LEPORELLA

Leporella A. S. George, *Nuytsia*, **1**, 18 (1971). Type species: *Leptoceras fimbriata* Lindl. (*Leporella fimbriata* (Lindl.) A. S. George).

Leptoceras Fitzg., *Austral. Orch.*, **2**, t. 4 (1889), *nom. illeg. non* (R.Br.) Lindl. (1840).

Derivation of name

From the Latin *lepus*, *leporis*, a hare, and *-ella*, a diminutive, referring to the resemblance of the flower to a small hare. **(DJ)**

Description (Plates 53, 54; Fig. 43.1)

Perennial geophytic *herbs*. *Roots* filamentous. *Tubers* ovoid, solitary, fleshy, naked; replacement tubers absent; daughter tubers formed on the end of slender stolonoid roots. *Stem* erect, short, unbranched, with a membranous cataphyll at the apical node. *Trichomes* absent from all parts except the labellum. *Leaves* one or two, basal, unequal, sessile; lamina ovate-lanceolate, coriaceous, convolute in bud, reddish around the main veins, margins entire; venation anastomosing. *Inflorescence* racemose, 1–3 flowered, erect, terminal; scape wiry, with one sterile bract; floral bracts foliaceous, sheathing. *Flowers* resupinate, dull-coloured, pedicellate; perianth firm to coriaceous. *Dorsal sepal* free, dissimilar to the lateral sepals, incurved over the column. *Lateral sepals* free. *Petals* free, erect, incurved, clavate, glandular, markedly dissimilar in size and shape to the sepals. *Labellum* free, attached by a small claw to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina obscurely three lobed, the anterior margins spreading and recurved, the distal margins deeply erose, all parts hairy; callus obscure; nectar absent. *Column* incurved, broadly winged; column foot reduced to a small bump; anther terminal, four-celled, persistent, basifixed, erect, papillate, rostrate; pollinia four, clavate, flat, mealy, naked, yellow; rostellum ventral; stigma entire, circular, concave. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, glabrous; sepals and petals persistent; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 43.2)

A monospecific genus endemic in southern Australia. **(DJ)**

Ecology

Leporella fimbriata, which is widely distributed across lowland areas of southern Australia between about 114° and 146° east, is strangely absent from Tasmania. Latitudinally it extends in a narrow band

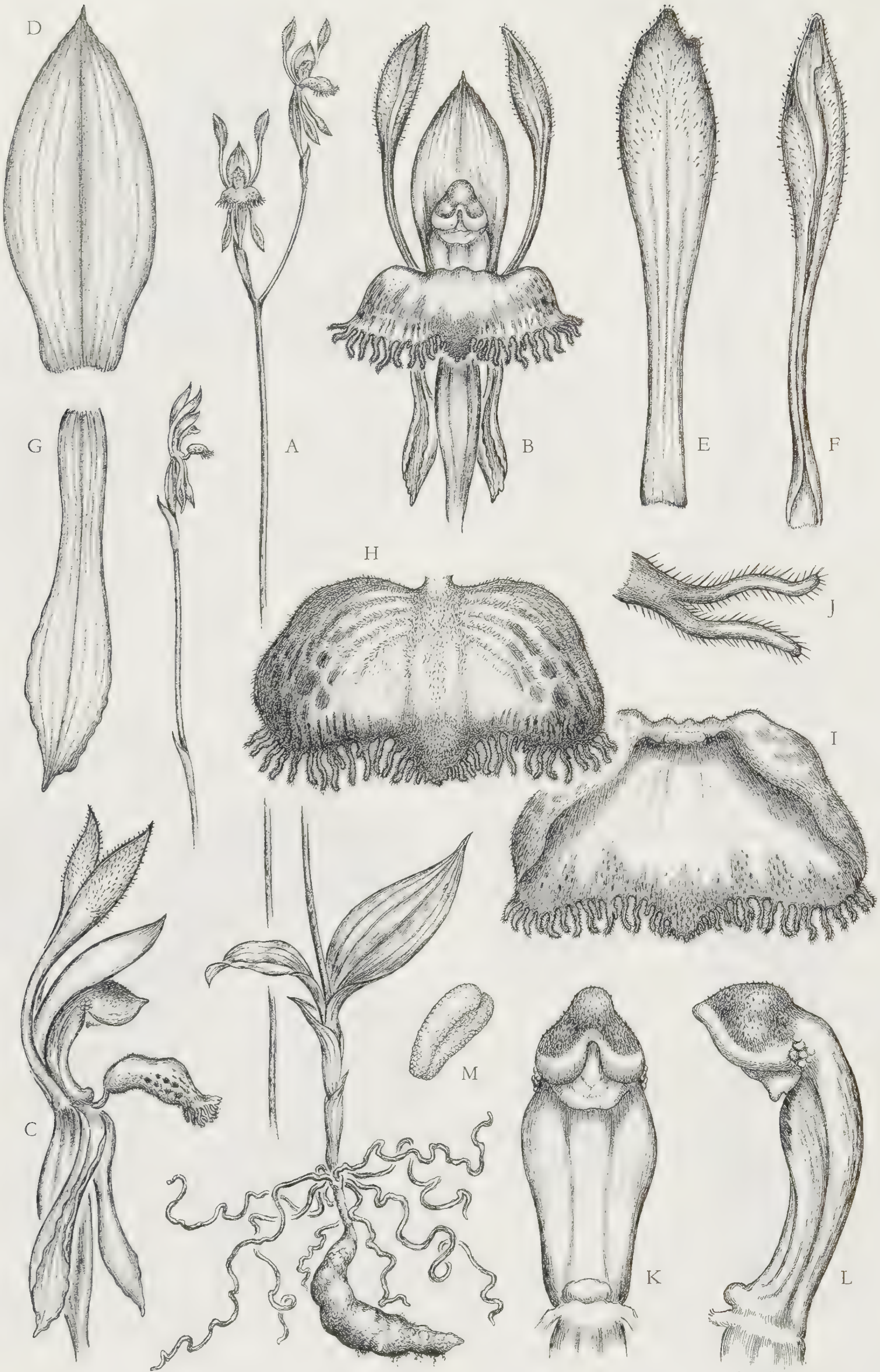

Fig. 43.1. *Leporella fimbriata* (Lindl.) A. S. George. A. Habit, ×1; B. Flower from front, ×4.5; C. Flower from side, ×4.5; D. Dorsal sepal, ×6; E. Petal from back, ×6; F. Petal from front, ×6; G. Lateral sepal, ×6; H. Labellum flattened, from above, ×6; I. Labellum from below, ×6; J. Marginal hairs from the labellum, ×21; K. Column from front, ×9; L. Column from side, ×9; M. Pollinia (two of four), ×21. Drawn by Oliver Q. Whalley.

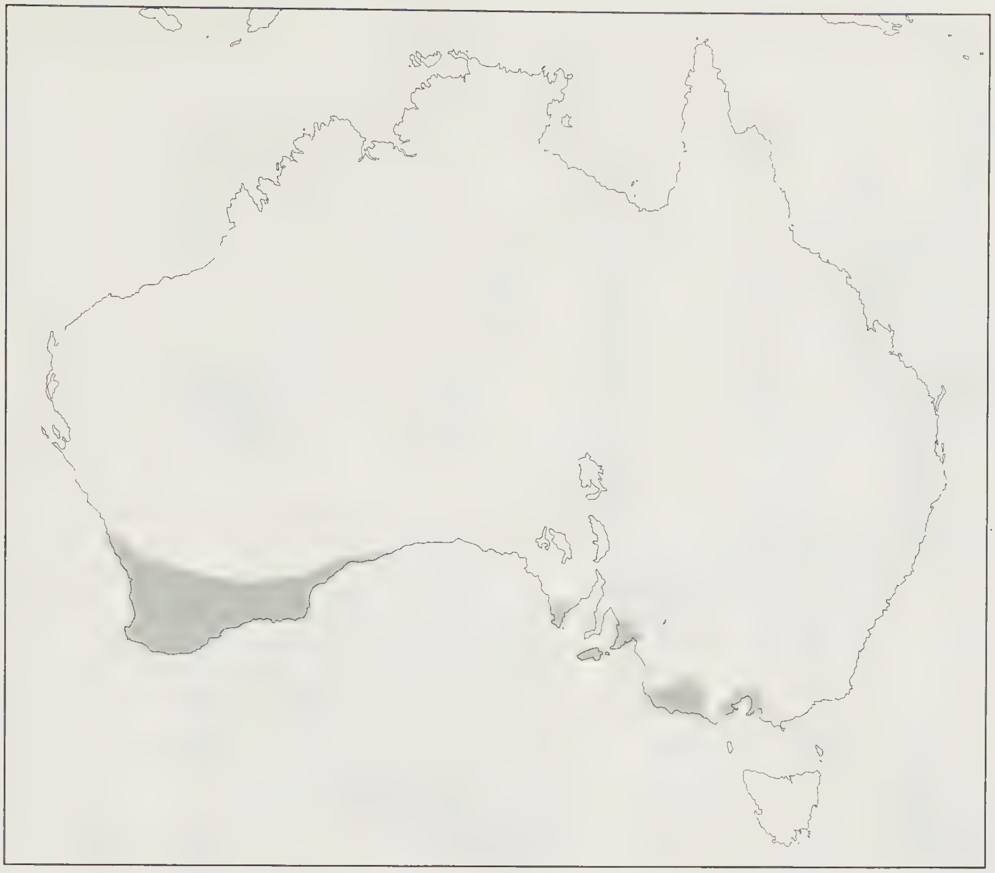

Fig. 43.2. Distribution map of *Leporella*.

between about 27°30′ south near Kalbarri in Western Australia and about 38°40′ south in southern Victoria. It is especially prominent in coastal and near-coastal heathlands and heathy forests, but it also occurs in sclerophyll forests, woodland, and shrubland, extending some distance inland but not to any significant elevation. It often inhabits nutrient-poor, deep acid sands but may also grow in sandy loams and laterite. It forms extensive clonal colonies and spreads locally by daughter tubers formed on the end of long stolonoid roots.

The climate in which this species grows is strongly seasonal, and plants grow actively in autumn and winter and survive as dormant tubers over summer. Flowering occurs in autumn and early winter. The perianth retains its integrity for many weeks after the stigma has become non-receptive. Flowering is strongly promoted by hot summer fires, especially in dense habitats. Dehiscence occurs 12–16 weeks after pollination. **(DJ)**

Pollination

Leporella fimbriata is unique among the Orchidaceae and all plants in being pollinated exclusively by sexually deceived male ants. Winged males of a bulldog ant species, *Myrmecia urens*, pollinate *L. fimbriata* as they attempt to copulate with the labellum (Bates 1979; Peakall 1989*b*). The following details of the pollination of *L. fimbriata* are taken from the comprehensive studies of Peakall (1984, 1989*b*), Peakall and James (1989), and Peakall *et al.* (1990).

Male *Myrmecia urens* are attracted to *L. fimbriata* flowers by odours emitted from glands on the tips of the erect petals. Peakall (1984, 1989*b*) found that males were attracted to detached petals but were not stimulated to copulate with them. Ants following the odour trail circle the flower or group of flowers before making a final upwind zigzag approach (Peakall 1989*b*). He interpreted the circling flight as an 'inspection flight'. However, it may simply represent a turning reaction after overshooting the scent source. Circling would enable the ant to regain the odour trail and make the final approach.

The ants land on the inflorescence, walk up to a flower, and align themselves sideways across the labellum below the column (Plate 54). In this position they open their genitalia and make probing movements with the abdomen inside the unfringed labellum margin. These movements push the thorax (and any pollinia it may be carrying) against the sticky stigmatic surface, effecting pollination. The friable pollen masses partially disintegrate and are smeared across the stigma.

Departing males twist forward below the anther, raise the anther flaps, and pick up pollinia on the centre of the thorax (Peakall 1989*b*). He believed that the twisting movement raised the pollinator's body into the stigma where it was smeared with viscous stigmatic secretion. As with *Caladenia* and *Chiloglottis* species, it seems more likely that the rostellum, despite its apparently rudimentary nature, is the source of glue for the pollinia. Pollinia are usually only removed from one side of the anther, so that at least two visits are needed to remove the full complement. This appears to be a consequence of the sideways orientation of the ants on the labellum; the set of pollinia removed apparently depends on whether the ant is facing left or right. Ants spend comparatively long periods on the labellum, from 1–10 minutes with a mean of 2.8 minutes. Multiple visits by pollinators to flowers could result in accumulation of a large pollen mass.

On leaving the labellum most ants crawl to the vertical petals and spend several minutes grooming before flying to nearby vegetation. After further resting they may fly to another *L. fimbriata* flower. Flight distances between successively visited flowers were relatively short, a mean of 3.1 m. About 70% of flights were within the boundaries of clones of *L. fimbriata*, indicating a high degree of self-pollination (Peakall and James 1989). However, genetic analyses showed adult population genetic structure did not reflect the high levels of selfing predicted. It appears that dispersal of light, wind-blown seeds, the 30% outcrossing rate, and possible elimination of selfed progeny reduce the effects of selfing.

Peakall (1989*b*) found that some flowers were more attractive than others; individuals may be visited up to four times, but the majority receive no visits at all. Pollination events within *Leporella* colonies tend to be highly episodic, lasting only one to several days. This seems to correlate with the short lifespan and flight periods of male *Myrmecia urens*. However, pollination episodes could occur anytime between late April and late June. The maximum number of potential pollination events per vector per day was three, indicating that each male performs few pollinations in its short lifetime. Males are mainly active between noon and 4 pm, with activity dependent on warm (18–26°C), fine weather.

The percentage of capsules setting seed varies considerably with season and site, with a maximum of 70%. Given that seed-set in artificially pollinated flowers of *L. fimbriata* is highly successful, it appears that seed-set in the field may be pollinator-limited due to low pollinator populations (Peakall 1989*b*).

Pollination of plants by ants is rare. One of the principal reasons for this appears to be that antibiotic substances, secreted from metapleural glands of ants as a defence against the spread of diseases in the close confines of the nest, are toxic to pollen grains (Beattie 1985; Peakall 1994). Studies by Peakall *et al.* (1990) showed that although male *M. urens* lack metapleural glands they nevertheless had toxic substances on their cuticles, probably derived from contact with worker ants, which have metapleural glands. However, tests showed that the viscous secretion of *L. fimbriata* used to secure the pollinia reduced the toxic effects, probably by providing a barrier between the cuticle and the pollinia. In addition, the aggregation of pollen in the pollinium itself minimizes contact by pollen with the cuticle so that most would remain viable. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Leporella plants have been maintained in cultivation for short periods of time only. **(HR)**

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44. LYPERANTHUS

Lyperanthus R.Br., *Prodr.*, 325 (1810). Type species: *Lyperanthus suaveolens* R.Br.

Fitzgeraldia F. Muell., *S. Sci. Rec.* **2**, 56, in obs. (1882). Type species: *Fitzgeraldia forrestii* F. Muell.

Derivation of name

From the Greek *lypros*, poor, wretched, and *anthos*, flower, in reference to the appearance or dull colours of these orchids. **(DJ)**

Description (Plate 55; Fig. 44.1)

Perennial geophytic *herbs. Roots* filamentous. *Tubers* ovoid, solitary, fleshy, naked; replacement tubers absent; daughter tubers formed on the end of long slender root-like stolons. *Stem* erect, short, unbranched, with a membranous cataphyll at the apical node. *Leaf* solitary, basal, sessile; lamina much longer than wide, erect, coriaceous, convolute in bud, hypostomatic, abaxial surface minutely papillate, waxy, margins incurved to involute; venation anastomosing. *Inflorescence* racemose, 1–few flowered, erect, terminal; scape wiry, with 1–3 sterile bracts; floral bracts foliaceous, sheathing. *Flowers* resupinate, dull-coloured, pedicellate; perianth firm to coriaceous. *Dorsal sepal* free, broader than the lateral sepals, cucullate over the column. *Lateral sepals* free. *Petals* free, subsimilar to the lateral sepals. *Labellum* free, attached by its base to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina three-lobed, curved, the proximal margins closely embracing the column, distal margins crenate or fimbriate; callus of proximal rows of imbricate calli, distally crowded, sessile to erect, papillate externally; nectar present. *Column* elongate, papillate

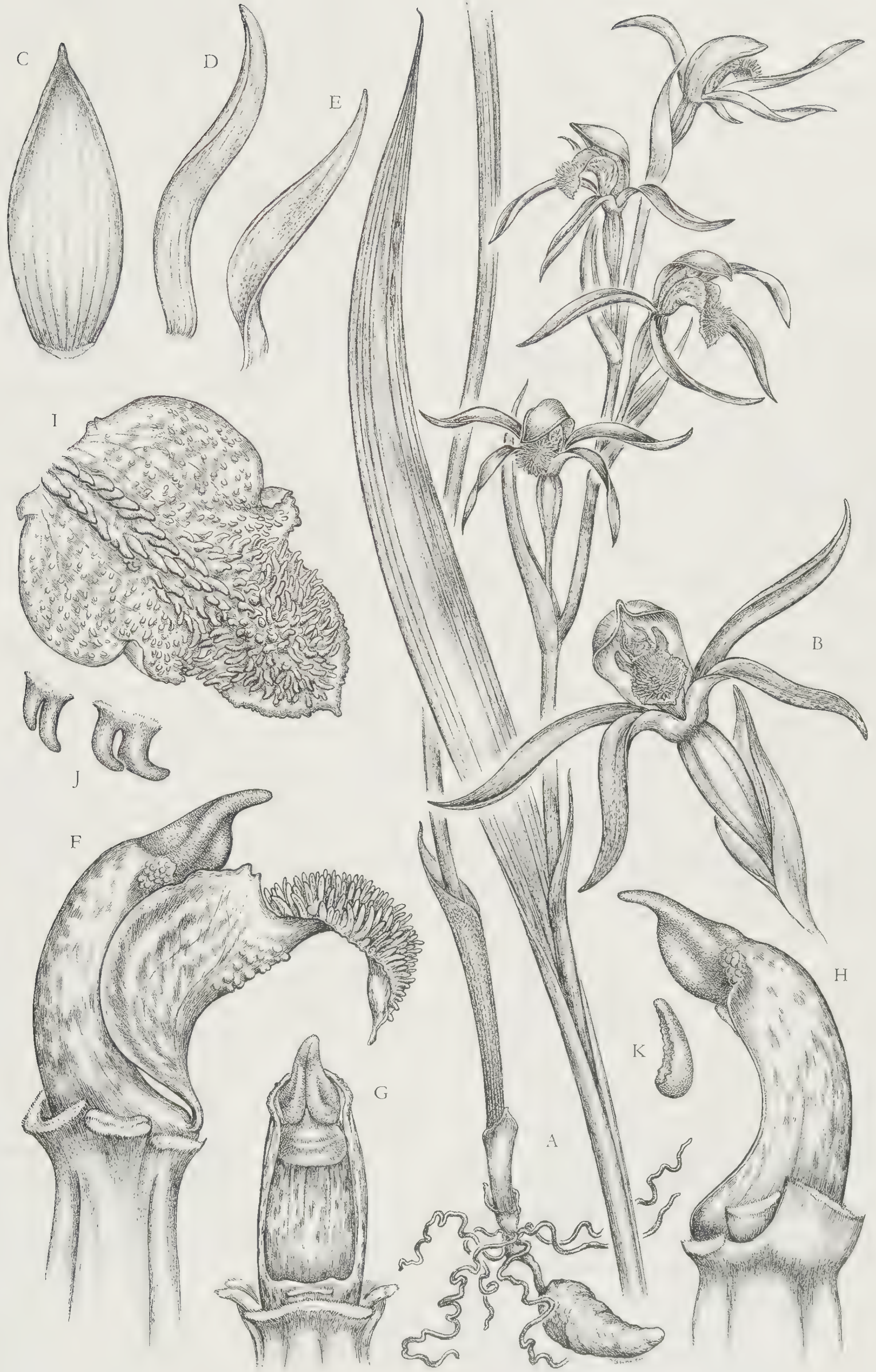

Fig. 44.1. *Lyperanthus serratus* Lindl. A. Habit and inflorescence, ×0.9; B. Flower from front, ×1.89; C. Dorsal sepal, ×2.7; D. Petal, ×2.7; E. Lateral sepal, ×2.7; F. Labellum and column from side, ×5.4; G. Column from front, ×5.4; H. Column from side, ×5.4; I. Labellum from above, ×5.4; J. Calli, labellum, ×8.1; K. Pollinium (one of four), ×5.4. Drawn by Oliver Q. Whalley from Kew Spirit Collection no. 47039.

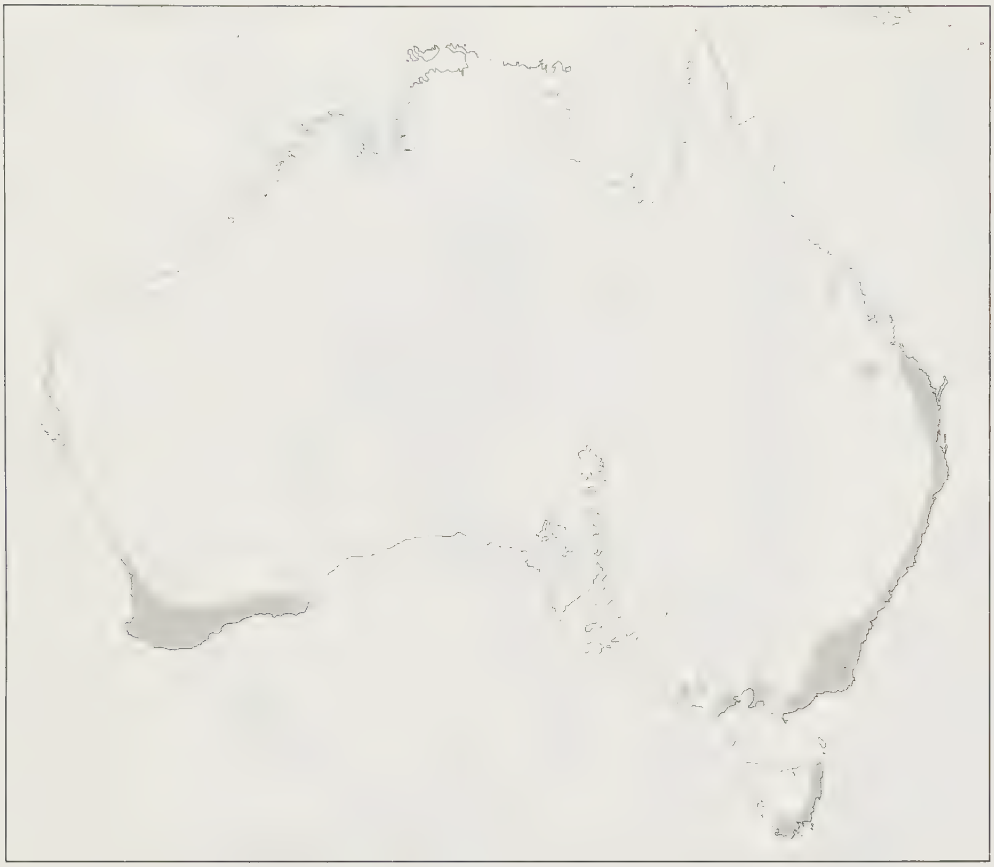

Fig. 44.2. Distribution map of *Lyperanthus*.

dorsally; wings narrow, fused throughout; column foot absent; anther terminal, four-celled, persistent, basifixed, erect, papillate, rostrate; pollinia four, clavate, flat, mealy, naked, yellow; rostellum ventral; stigma entire, circular, concave. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, glabrous, erect; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 44.2)

A genus of two species endemic in southern Australia and Tasmania. **(DJ)**

Ecology

Both species of *Lyperanthus* are terrestrials that occur in widely spaced, loose groups or sparse colonies, reproducing both sexually from seed and clonally by the production of daughter tubers on the end of long root-like stolons. *Lyperanthus suaveolens* R.Br., from eastern Australia, is distributed from about 24°50′ south in the Carnarvon Ranges, Queensland, to about 43° south in southern Tasmania. It ranges from near sea level to about 1000 m. In Western Australia, *L. serratus* has a more restricted lowland distribution between about 31°30′ south and 35° south. Habitats include open forest, woodland, shrubland, and heathland, usually in well-drained sandy or clay loams.

Both species occur in areas that have a strong seasonal climate, and the plants have periods of active growth and dormancy. Active growth occurs in autumn/winter. The leaves of both species are fully expanded prior to flowering, which occurs in spring and is not greatly influenced by the incidence of fire. Seed dispersal in both species occurs 8–12 weeks after pollination. The plants survive the summer extremes of heat, dryness, and low humidity as dormant tubers. **(DJ)**

Pollination

Nothing is known about the pollination of *Lyperanthus* species. *Lyperanthus suaveolens* is strongly fragrant in warm weather (Jones 1988; Backhouse and Jeanes 1995), a feature indicating it may be pollinated by nectar-seeking bees. However, unlike most bee-pollinated flowers, both *Lyperanthus* species have a dull-coloured perianth and are relatively inconspicuous. The labellum apices of both species are more prominent and may be pollen or stamen mimics. *Lyperanthus serratus* has dense yellowish to reddish hairs, and *L. suaveolens* has a bright yellow coloration. Both may be attractive to bees. In addition, the base of the labellum and its upturned side lobes form a floral tube with the column and nectar is present, characteristic of many bee-pollinated flowers. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

The eastern Australian species *Lyperanthus suaveolens* is much more widely cultivated than the western Australian *L. serratus*, probably only because of availability.

Mix: basic. Light: 50%. Watering: early autumn to late spring. Flowering: the tuber needs to be good size before it will flower. Propagation: colony-formers, multiplication rate ×1.5 on average. **(HR)**

Taxonomic literature

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45. MEGASTYLIS

Megastylis (Schltr.) Schltr., *Bot. Jahrb.*, **45**, 379, 384 (1911). Type species: *Caladenia gigas* Rchb.f. (*Megastylis gigas* (Rchb.f.) Schltr.).

Lyperanthus R.Br. sect. *Megastylis* Schltr., *Bot. Jahrb.*, **39**, 43 (1906).

Derivation of name

From the Greek *megas*, large, and *stylos*, pillar, column, referring to the large column found in these orchids. **(DJ)**

Description (Plate 56; Fig. 45.1)

Perennial, terrestrial or semi-lithophytic evergreen clump-forming *herbs. Roots* fleshy, glabrous or covered with numerous short root hairs. *Tubers* absent. *Stems* erect, short, unbranched; vertical shoots with fibrous, clathrate or foliaceous cataphylls at each node. *Trichomes* mostly absent, if present glandular (*M. glandulosa*). Leaves 1–few per shoot, basal, petiolate, erect to arcuate; petioles channelled; lamina mostly ovate-lanceolate, coriaceous, convolute in bud, margins entire or with minute black teeth (*M. paradoxa* (Kränzlin) N. Hallé); venation anastomosing. *Inflorescence* racemose, several–many flowered, erect to arcuate, terminal; scape sturdy, with several foliaceous sterile bracts; floral bracts foliaceous, sheathing or spreading. *Flowers* resupinate, dull-coloured, crowded, pedicellate; perianth firm to coriaceous. *Dorsal sepal* free, broader than or similar to the lateral sepals, cucullate over the column. *Lateral sepals* free or fused at the base (*M. glandulosa*). *Petals* free or fused marginally (*M. glandulosa*), smaller or larger than the lateral sepals (*M. glandulosa*). *Labellum* free, attached by a short claw to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina undivided; callus of irregular rows of papilla-like calli, with or without a thickened ruminate basal concrescence, or of an unadorned, thickened central band (*M. glandulosa*); nectar absent or present (*M. glandulosa*). *Column* elongate, incurved; wings narrow, fused throughout; column foot absent; anther terminal, two-celled, persistent, basifixed, erect, papillate, non-rostrate; pollinia two, naked, clavate, flat, mealy, cream to light yellow; rostellum ventral; stigma entire, circular, concave. *Ovary* elongate, ribbed, glabrous or glandular hairy. *Capsules* dehiscent, glabrous, erect; sepals and petals persistent; pedicels not elongating in fruit. *Seeds* numerous, light- or dark-coloured, winged. **(DJ)**

Distribution (Fig. 45.2)

A genus of seven species, six endemic to New Caledonia, including Isle des Pines, and one, *M. gigas*, also occurring on Anatom Island, Vanuatu. **(DJ)**

Ecology

Megastylis is a narrow endemic with a limited latitudinal range extending from about 20°10′ south on Anatom to about 22°50′ south on the Isle des Pines. Species are distributed from the lowlands at about sea level up to 1600 m in the mountains. All species are found in regions of ultrabasic rock formation, growing as terrestrials on or among the rocks themselves. They occur as individuals or form localized crowded clumps and reproduce solely from seed. Some species, such as *M. gigas*, *M. latilabris* (Schltr.) Schltr., and *M. rara* (Schltr.) Schltr., grow in full sunlight in sparse maquis and scrubland often on rocky sites, whereas others, including *M. latissima* (Schltr.) Schltr., *M. montana* (Schltr.) Schltr., and *M. glandulosa* grow in rainforest or dense scrubland. *Megastylis glandulosa* has also been recorded from grassland. Seeds of *Megastylis* species take 10–16 weeks to mature after pollination. **(DJ)**

Pollination

There appears to be no published information on the pollination of *Megastylis*. The flowers exhibit features characteristic of bee-

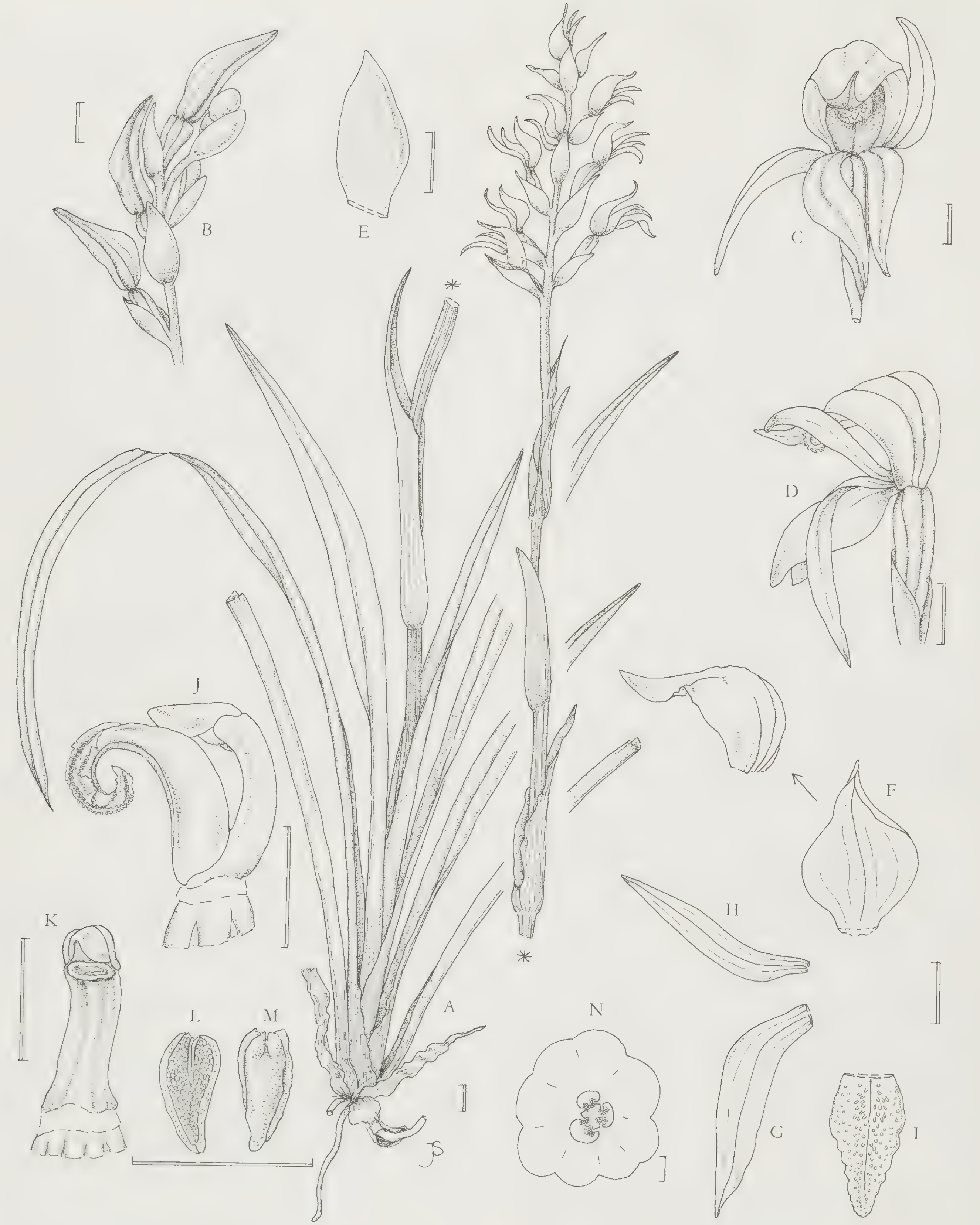

Fig. 45.1. *Megastylis gigas* (Rchb.f.) Schltr. A. Habit. Entire root system not seen; B. Immature inflorescence; C. Flower, front vew; D. Flower, side view; E. Bract; F. Dorsal sepal; G. Lateral sepal; H. Petal; I. Labellum; J. Labellum and column, side view; K. Column, front view; L. Anther and anther-cap from below; M. Anther cap, from above. N. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *MacKee 37953*, *Vieillard 1301*, and Kew Spirit Collection no. 54279.

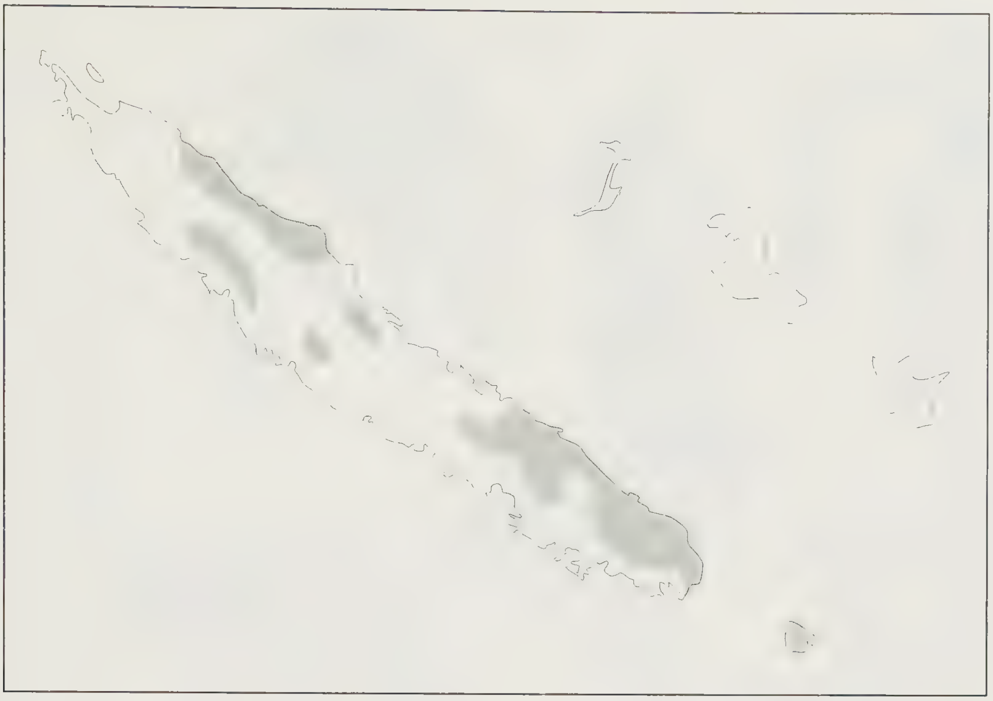

Fig. 45.2. Distribution map of *Megastylis.*

pollination syndromes (van der Pijl and Dodson 1966). The labellum has upturned margins, forming a floral tube with the large hooded dorsal sepal. It is likely bees enter the tube seeking nectar at the base of the labellum. The downturned labellum apex provides a landing platform at the entrance to the floral tube, and calli on the labellum of most species may be pollen mimics. Nectar is known to be provided only in *M. glandulosa.* No information is available on whether there is any scent. The lateral sepals and petals radiate from the centre of the flower below the labellum in a manner similar to the bee-pollinated *Caladenia* species of section *Caladenia.* They provide an attractive display and probably guide bees to the centre of the flower. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Nothing is known about cultivating *Megastylis.* **(HR)**

Taxonomic literature

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46. PYRORCHIS

Pyrorchis D. L. Jones & M. A. Clem., *Phytologia,* **77 (6),** 448 (1994). Type species: *Lyperanthus nigricans* R.Br. (*Pyrorchis nigricans* (R.Br.) D. L. Jones & M. A. Clem.).

Derivation of name

From the Greek *pyr,* fire, and *orchis,* orchid, referring to the dramatic influence that summer fires have on flowering in these orchids. **(DJ)**

Description (Plate 57; Fig. 46.1)

Perennial geophytic *herbs. Roots* filamentous. *Tubers* ovoid, solitary, fleshy, naked; replacement tubers absent; daughter tubers formed on the end of long slender root-like stolons. *Stem* erect, short, unbranched, with a membranous cataphyll at the apical node. *Trichomes* absent or reduced to papillae. *Leaves* 1–3, basal, unequal, sessile; lamina mostly prostrate, coriaceous, convolute in bud, amphistomatic, both surfaces minutely papillate, margins entire; venation anastomosing. *Inflorescence* racemose, 1–few flowered, erect, terminal; scape wiry, with 1–3 sterile bracts; floral bracts foliaceous, loosely sheathing. *Flowers* resupinate, dull-coloured, pedicellate; perianth firm to coriaceous. *Dorsal sepal* free, broader than the lateral sepals, cucullate over the column. *Lateral sepals* free. *Petals* free, subsimilar to the lateral sepals. *Labellum* free, attached by its base to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina obscurely three-lobed, curved, the proximal margins closely embracing the column, distal margins crenate or erose, papillate externally; callus with a low central ridge and irregularly arranged sessile calli; nectar present.

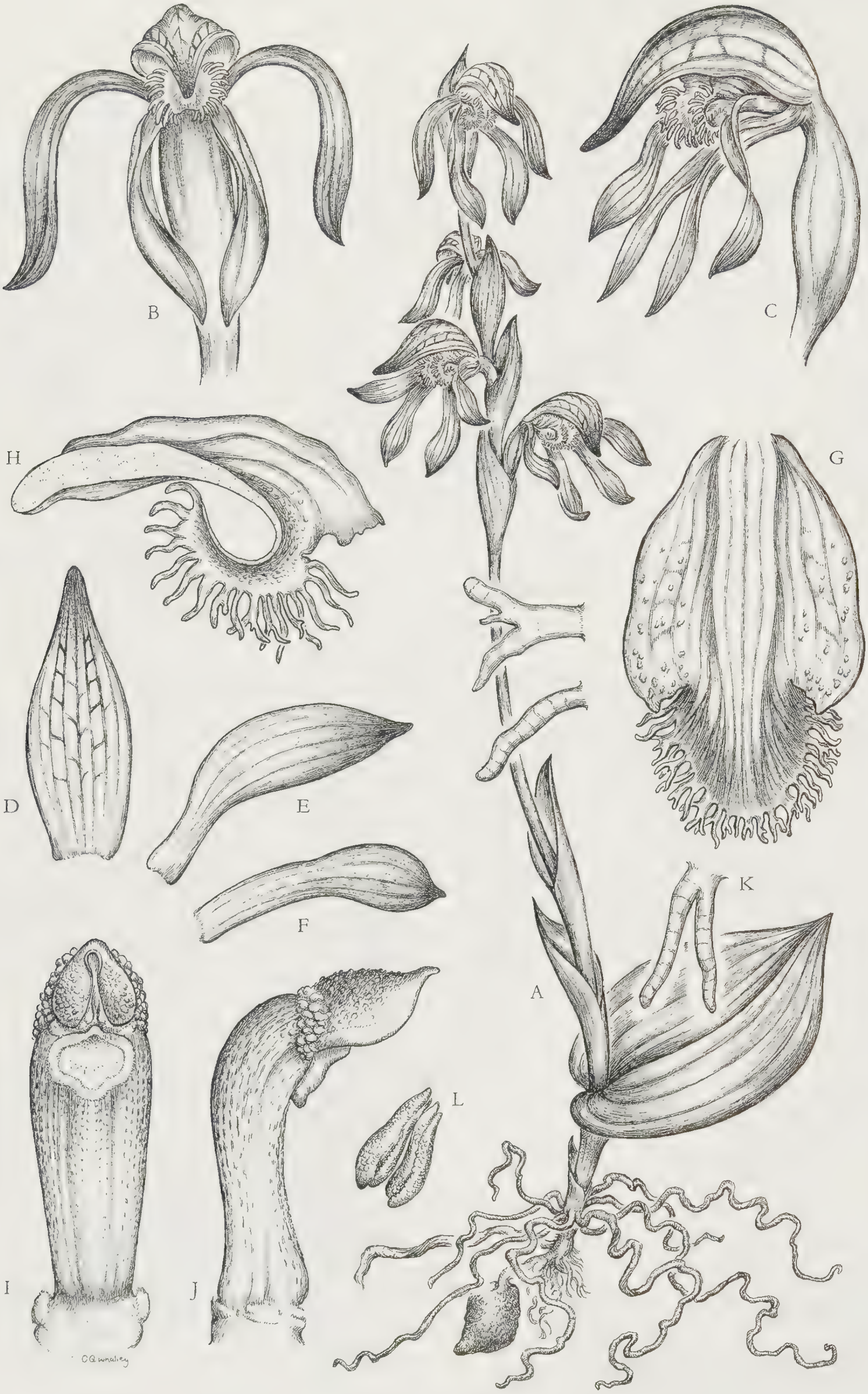

Fig. 46.1. *Pyrorchis nigricans* (R.Br.) D. J. Jones & M. A. Clem. A. Habit, ×1; B. Flower from front, ×3; C. Flower from side, ×3; D. Dorsal sepal, ×3; E. Petal, ×3; F. Lateral sepal, ×3; G. Labellum flattened out, from above, ×6; H. Labellum, longitudinal section, ×9; I. Column from front, ×6; J. Column from side, ×6; K. Labellum, marginal hairs, ×21; L. Pollinia, ×15. Drawn by Oliver Q. Whalley.

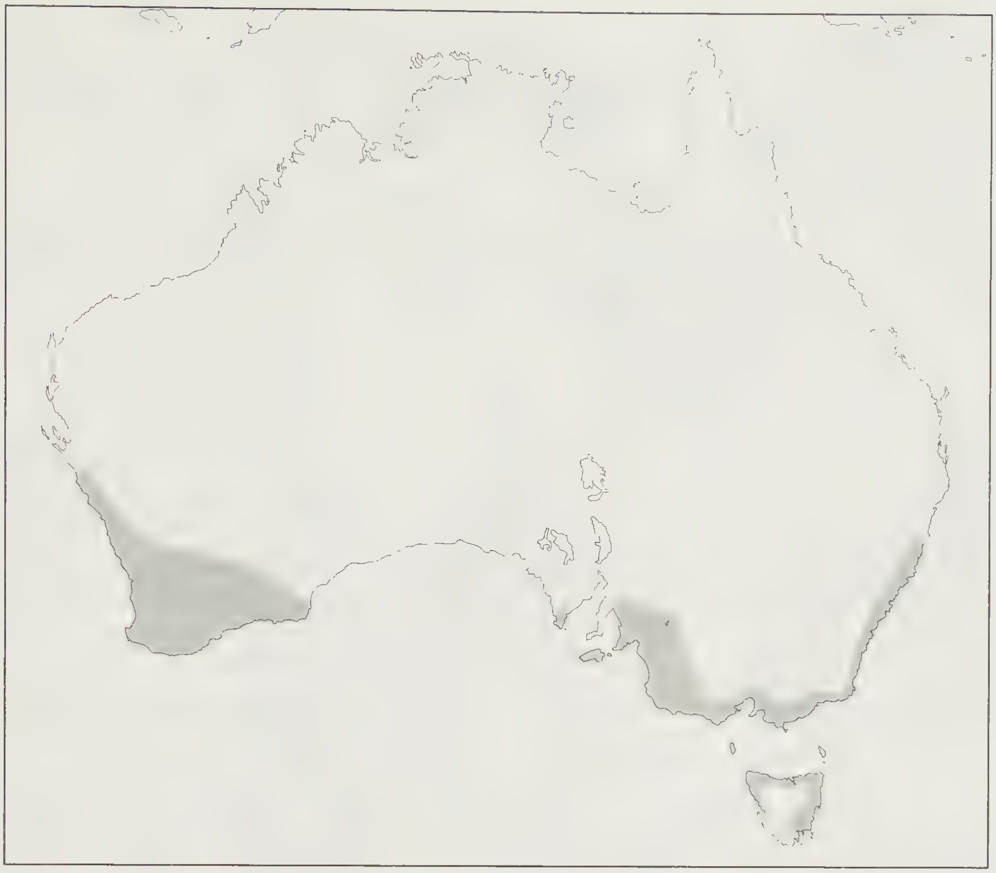

Fig. 46.2. Distribution map of *Pyrorchis.*

Column elongate, nearly straight, papillate dorsally; wings narrow, fused throughout; column foot absent; anther terminal, four-celled, persistent, basifixed, erect, papillate, rostrate; pollinia four, clavate, flat, mealy, naked, yellow; rostellum ventral; stigma entire, circular, concave. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, glabrous, erect; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 46.2)

A genus of two species endemic in south-eastern and south-western Australia and Tasmania. **(DJ)**

Ecology

Pyrorchis nigricans has an interesting distribution, widespread in southern Australia on the east and west coasts. In the west it occurs from the southern coast at about 35° south northward to 26° south near Shark Bay. By contrast, in eastern Australia the same species is distributed between 32°24′ south at Bungwahl, New South Wales, and 43° south in southern Tasmania. The other species, *P. forrestii* (F. Muell.) D. L. Jones & M. A. Clem., has a much more limited distribution, being restricted to Western Australia between about 33°30′ south and 35° south. Both species are terrestrials that occur in sparse to dense colonies and reproduce sexually from seed and by the production of daughter tubers on the end of long root-like stolons.

They are found in areas that have a strong seasonal climate, with the plants growing actively in autumn and winter and flowering in spring and early summer. Flowering in undisturbed habitats is rare or absent, but dramatic mass flowering events follow hot summer fires, especially where there have been long intervals between burns. Habitats of *P. nigricans* include open forest, woodland, shrubland, heathy forest, and heathland. In Western Australia it often grows on large granite outcrops. Whereas this species usually grows in well-drained soils, *P. forrestii*, which is usually found in densely forested habitats, commonly grows in seasonally wet peaty soils around the margins of swamps and along drainage lines. Dispersal of seed begins 12–16 weeks after pollination. **(DJ)**

Pollination

Scientific studies on the pollination of *Pyrorchis* are lacking, and there appears not to be many published casual observations. Both *Pyrorchis* species emit an intense sweet perfume on warm days (Hoffman and Brown 1992), although Bates and Weber (1990) state the flowers may be odourless or only faintly scented with a sickly sweet or fox-like odour. Hoffman and Brown reported that both *P. nigricans* and *P. forrestii* secrete small amounts of nectar at the base of the column. The sweet odour, presence of nectar, and the floral tube formed by the labellum and column indicate *Lyperanthus* species are pollinated by bees. According to Jones (1988), *P. nigricans* is pollinated by a bee that forces its way down the floral tube. Only *P. forrestii* has brightly coloured flowers typical of bee-pollinated plants. It also has prominent radiating red stripes on the labellum apex, which may function as nectar guides. The flowers of *P. nigricans* are darkened by heavy reddish maroon perianth segments and stripes on the hood-like dorsal sepal. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Mix: basic with extra coarse sand to improve drainage. Light: 50% shade. Watering: early autumn to late spring. Flowering: spectacular flowering occurs in the wild after hot summer fires. In cultivation, flowering is poor, and only limited experiments to stimulate flowering have been carried out. Propagation: colony-formers, multiplication rate ×2. Limited experience with *Pyrorchis forrestii.* **(HR)**

Taxonomic literature

Backhouse, G. and Jeanes, J. (1995). *The orchids of Victoria.* Miegunyah Press, Carlton, Victoria.

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47. RIMACOLA

Rimacola Rupp, *Victorian Naturalist,* **58**, 188 (1942). Type species: *Lyperanthus ellipticus* R.Br. (*Rimacola elliptica* (R.Br.) Rupp).

Derivation of name

From the Latin *rima*, a cleft or fissure, and *-cola*, inhabiting, dwelling, referring to this orchid's habitat of cracks, clefts, and fissures in rocks. **(DJ)**

Description (Plate 58; Fig. 47.1)

Perennial epilithic, evergreen *herbs. Roots* fleshy, glabrous. *Tubers* absent. *Stems* erect, short, branched, forming clumps; vertical shoots with membranous cataphylls at each node. *Trichomes* absent or reduced to papillae. *Leaves* few per shoot, basal and petiolate or subcauline and sessile; petioles channelled; lamina mostly ovate-lanceolate, erect to arcuate, coriaceous, convolute in bud, margins entire; venation anastomosing. *Inflorescence* racemose, several-flowered, arcuate, terminal; scape wiry, with 1–2 sterile bracts; floral bracts foliaceous, spreading. *Flowers* resupinate, dull-coloured, pedicellate; perianth firm to coriaceous, papillate. *Dorsal sepal* free, broader than the lateral sepals, cucullate over the column. *Lateral sepals* free. *Petals* free, smaller than the lateral sepals. *Labellum* free, attached by its base to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina obscurely three-lobed or undivided, closely embracing the column, the margins with an irregular band of hyaline cells; callus a basal plate with irregular low parallel ridges; nectar absent. *Column* elongate, incurved; wings narrow, fused throughout; column foot absent; anther terminal, four-celled, persistent, basifixed, erect, papillate, rostrate; pollinia four, clavate, flat, mealy, naked, yellow; rostellum ventral; stigma entire, circular, concave. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, glabrous, erect; sepals and petals persistent; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 47.2)

A monospecific genus endemic to a narrow range in eastern Australia. **(DJ)**

Ecology

Rimacola elliptica is primarily lithophytic, dwelling in the moist cracks and crevices of sheltered gorges and cliffs, less commonly on large sandstone outcrops on forested, southern slopes. Plants are evergreen, forming localized, congested clumps that flower in late spring and early summer. Reproduction is solely from seed, dispersal of which begins 16–20 weeks after pollination. Latitudinally this species has a narrow distribution, confined to the central parts of New South Wales between about 33°30′ south and 34°30′ south. It is most prominent in mountainous regions up to about 800 m and descends to lower elevations in some areas near the coast. **(DJ)**

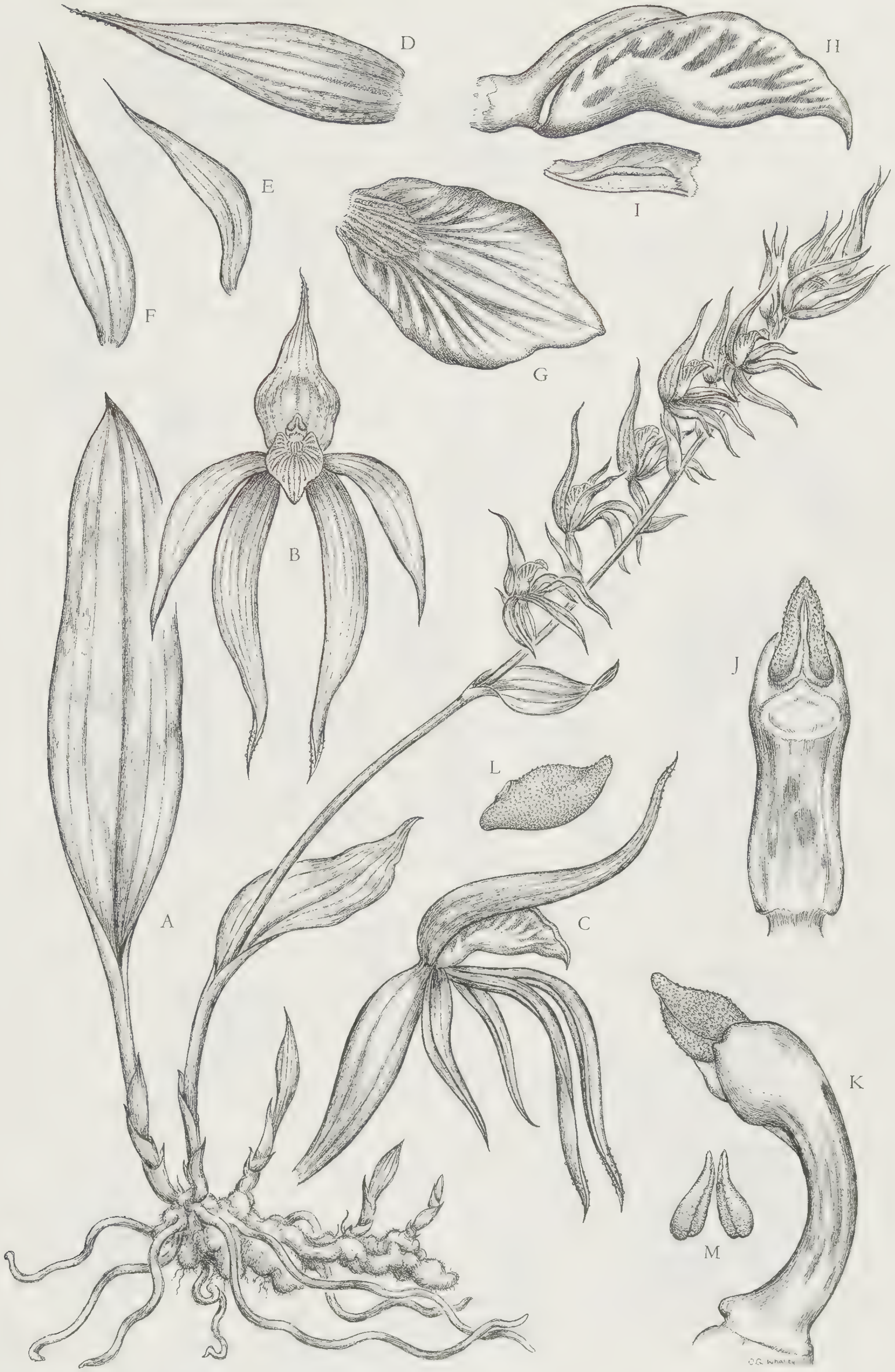

Fig. 47.1. *Rimacola elliptica* (R.Br.) Rupp. A. Habit, ×1; B. Flower from front, ×3; C. Flower from side, ×3; D. Dorsal sepal, ×3; E. Petal, ×3; F. Lateral sepal, ×3; G. Labellum from above, ×6; H. Labellum and column from side, ×6; I. Labellum callus, longitudinal section, ×9; J. Column from front, ×9; K. Column from side, ×9; L. Anther with anther cap, ×9; M. Pollinia, ×9. Drawn by Oliver Q. Whalley after W. H. Nicholls (1969).

Fig. 47.2. Distribution map of *Rimacola*.

Pollination

Little is known of the pollination of *R. elliptica*. There are no reports of nectar production or emission of a scent. The flowers are an inconspicuous light green colour with a pale creamy white labellum having reddish markings. The labellum calli are mostly reduced to a cluster of papillae at the base. Floral structure and coloration do not obviously conform to any recognized pollination syndrome.

Cady and Rotherham (1970) stated that *R. elliptica* is not self-pollinating because only three flowers out of 38 developed seed capsules in herbarium pressings. Jones (1988) stated that pollination is effected by a small black wasp but gives no further details.

The pollination mechanism is probably similar to that of other Caladeniinae. The upturned side lobes of the labellum form a floral tube with the hooded dorsal sepal and column. The pollinator would move to the base of the tube and effect pollination as it retreated, first depositing pollinia from its thorax onto the stigma, receiving a coating of glue, and finally opening the one-way anther flaps to contact the pollinia. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Rimacola plants are difficult to maintain in cultivation. **(HR)**

Taxonomic literature

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48. WAIREIA

Waireia D. L. Jones, M. A. Clem. & Molloy, *Orchadian*, **12**, 282 (1997). Type species: *Thelymitra stenopetala* Hook.f. (*Waireia stenopetala* (Hook.f.) D. L. Jones, M. A. Clem. & Molloy).

Derivation of name

From the Maori *wai*, water, and *rei*, swampy ground, peat, referring to the wet peaty substrates in which this orchid usually grows. **(DJ)**

Description (Plate 59; Fig. 48.1)

Perennial geophytic *herbs*. *Roots* filamentous. *Tubers* ovoid, solitary, fleshy, naked; replacement tubers produced on the end of short

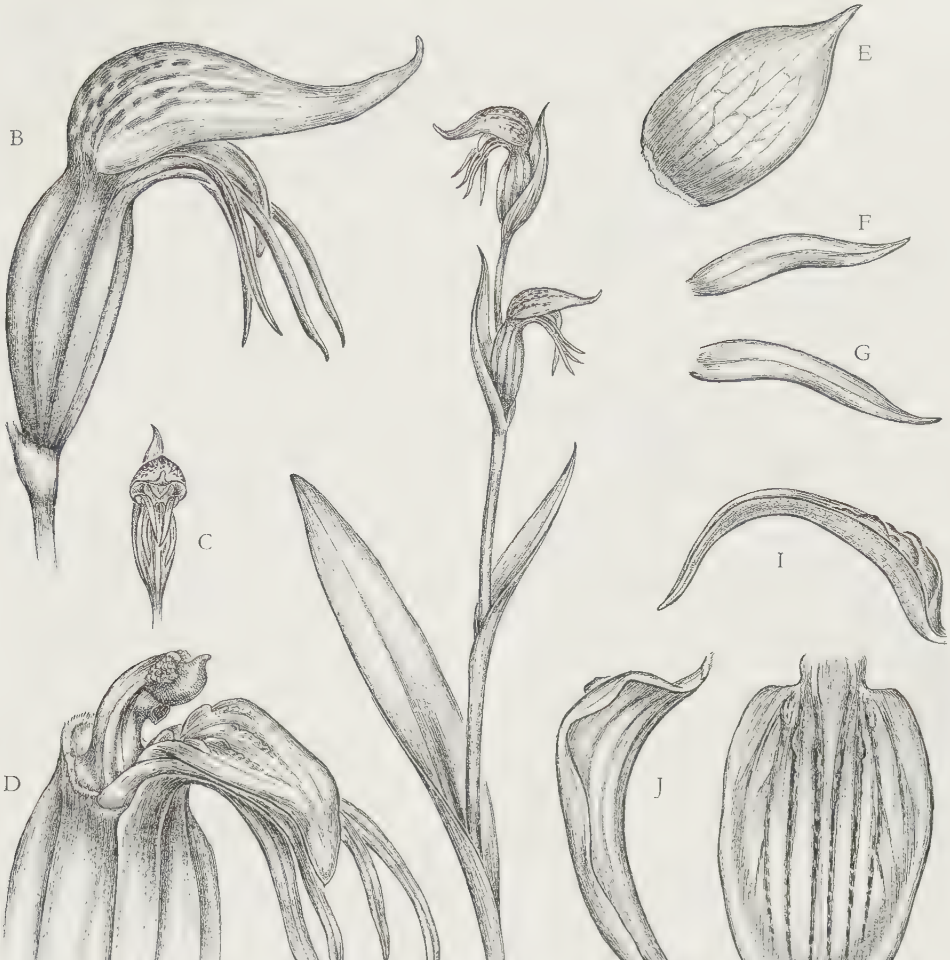

Fig. 48.1. *Waireia stenopetala*. A. Habit, ×0.9; B. Flower from side, ×5.4; C. Flower from front, ×0.9; D. Flower, oblique view (dorsal sepal removed), ×5.4; E. Dorsal sepal, ×2.7; F. Petal, ×2.7; G. Lateral sepal, ×2.7; H. Labellum, flattened, ×8.1; I. Labellum, longitudinal section, ×8.1;J. Labellum from side, ×8.1; K. Column from front, ×10.8; L. Column apex from above, ×10.8; M. Column from side, ×10.8. Drawn by Oliver Q. Whalley from Kew Spirit Collection no. 36978.

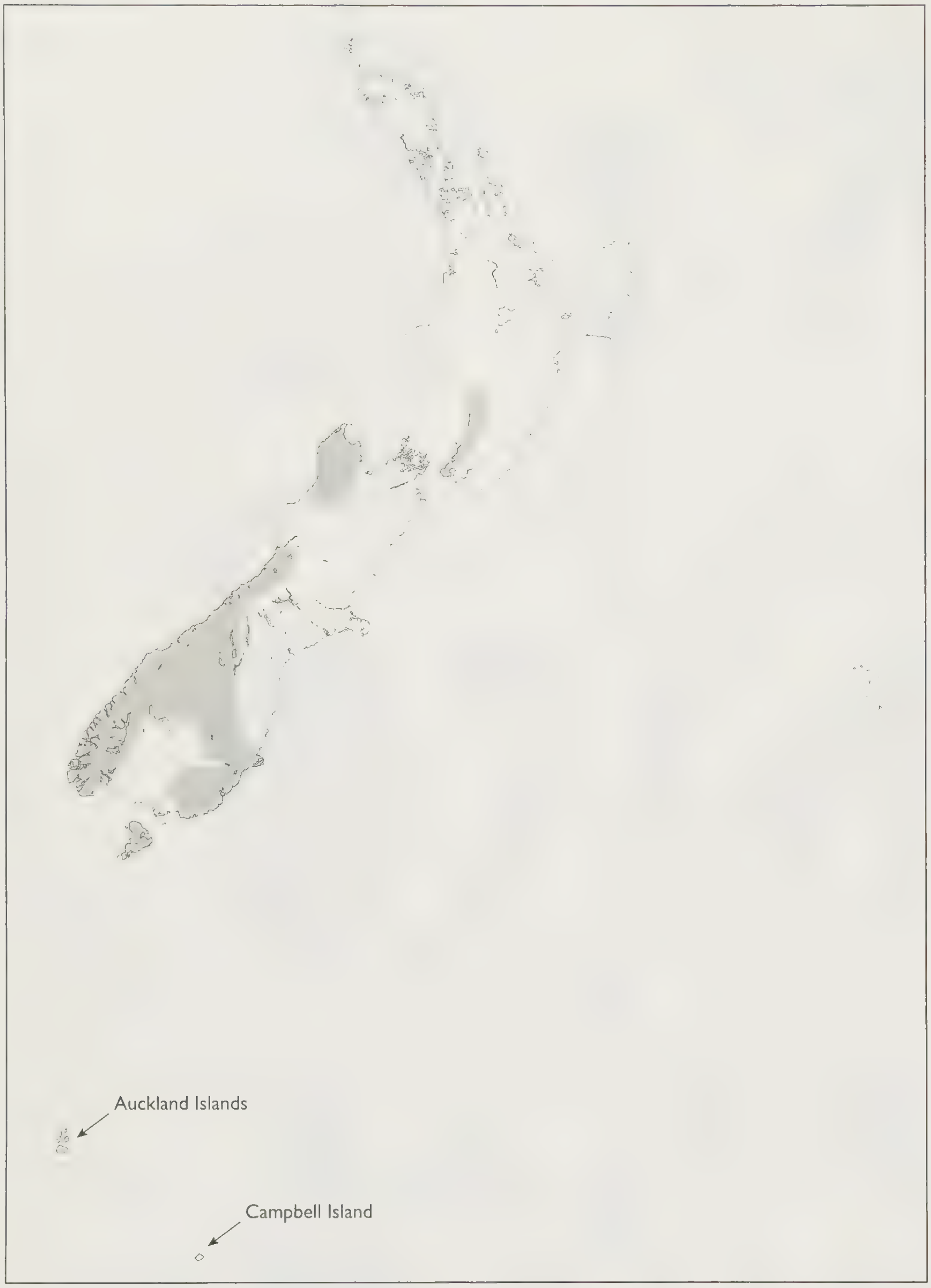

Fig. 48.2. Distribution map of *Waireia*.

droppers; daughter tubers formed on the end of slender root-like stolons. *Stem* erect, short, unbranched, with membranous cataphylls at each node. *Trichomes* absent. *Leaf* solitary, basal, sessile on flowering plants, petiolate on sterile plants; lamina much longer than wide, erect, coriaceous, convolute in bud, margins entire; venation anastomosing. *Inflorescence* racemose, 1–few flowered, erect, terminal; scape wiry, with one sterile bract; floral bracts foliaceous, sheathing. *Flowers* resupinate, dull-coloured, pedicellate; perianth firm to coriaceous. *Dorsal sepal* free, much broader than the lateral sepals, strongly cucullate over the column. *Lateral sepals* free. *Petals* free, subsimilar to the lateral sepals. *Labellum* free, attached by a short claw to the anterior column base, markedly dissimilar in size and shape to the sepals and petals, ecalcarate; lamina undivided, recurved, not closely embracing the column, margins slightly irregular; callus of low parallel ridges; nectar absent. *Column* elongate, incurved, narrowly winged, papillate dorsally; column foot absent; anther terminal, four-celled, persistent, basifixed, erect, papillate, rostrate; pollinia four, clavate, flat, mealy, naked, yellow; rostellum ventral; stigma entire, circular, concave. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, glabrous, erect; sepals and petals persistent; pedicels not elongating in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 48.2)

A monospecific genus endemic in New Zealand, including the southern part of the North Island, western and southern parts of the South Island and Stewart Island, Auckland Islands, and Campbell Islands. **(DJ)**

Ecology

Latitudinally, *Waireia* is distributed from about 41° south in the Tararua Range of New Zealand's North Island to about 52° south on Campbell Island. It ranges from 500 m to about 1500 m on New Zealand's main islands, descending to sea level on Stewart Island and the subantarctic islands. It grows in a range of poorly drained peaty soils, moraines, and cushion bogs. In upland montane and subalpine areas it grows in meadows, tussock grassland, and tussock shrubland; in the subantarctic islands it grows in grassland and restionaceous herbfield. Plants usually occur in sparse colonies and reproduce both vegetatively by the production of daughter tubers on the end of root-like stolons and from seed. Flowering occurs between November and March, and seed dispersal begins 10–14 weeks after pollination. **(DJ)**

Pollination

Waireia stenopetala is thought to be self-pollinating (Thomson 1879; Molloy 1990; Jones *et al.* 1997). The green, inconspicuous flowers do not seem adapted for pollinator attraction and are often closed. Thomson (1879) found the rostellum was only slightly viscid, and no pollinaria were removed from the 39 flowers he examined. The pollen masses were incoherent, and in older flowers pollen grains were scattered over the stigma below the anther with the ovaries well developed. Jones *et al.* (1997) noted that abundant seed capsules are formed each season, a characteristic of autogamous species. Since some flowers appear to self-pollinate without opening, *W. stenopetala* seems to be at least partially cleistogamous. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Not known in cultivation. **(HR)**

Taxonomic literature

Johns, J. and Molloy, B. (1983). *Native orchids of New Zealand.* A. H. & A. W. Reed, Wellington.

Jones, D. L., Clements, M. A., and Molloy, B. P. J. (1997). *Waireia*, a new genus of Orchidaceae from New Zealand. *Orchadian*, **12**, 282–7.

Moore, L. and Edgar, E. (1970). *Flora of New Zealand*, Vol. 2. Government Printer, Wellington.

SUBTRIBE PRASOPHYLLINAE

Prasophyllinae Schltr., *Bot. Jahrb. Syst.*, **45**, 381 (1911). Type: *Prasophyllum* R.Br.

Tribe *Microtideae* Szlach., *Fragm. Flor. Geobot.* **36**, 36 (1991).

Subtribe *Microtidinae* (Szlach.) Szlach., *Fragm. Flor. Geobot. Suppl.* **3**, 20 (1995). Type: *Microtis* R.Br.

Description

Glabrous, tuberous geophytic *herbs*. *Tubers* globose to elongate, naked. *Leaf* solitary, cylindrical, terete, sessile, erect. *Inflorescence* racemose or spicate. *Flowers* resupinate or non-resupinate, dull-coloured; tepals dissimilar. *Labellum* unlobed, either fixed to the base of the column or hinged to the apex of the column foot; lamina either with a prominent callus plate or enlarged areas of callus; nectar present. *Column* short; column foot present or not; pollinarium present; pollinia four. *Fruit* a dehiscent capsule. **(DJ)**

Anatomy

Leaf

SURFACE

Hairs adaxial in many species of *Prasophyllum*, 2–5 celled, filamentous, unbranched, glandular, clustered; hairs unicellular or bicellular on adaxial surface of bract of *Genoplesium*, absent in *Microtis*. Epidermis: adaxial epidermis often dissociated in *Microtis* and *Prasophyllum*. Abaxial epidermal cells elliptical, rectangular to polygonal, often axially elongated; walls thin to thick, depending on species. Stomata on abaxial surface only; absent in *Genoplesium*.

TRANSECTION

Terete, sheathing, in *Prasophyllum* grading to ± dorsiventral, grooved on free portion at apex. Cuticle thin, smooth to striate. Epidermis: adaxial cells (where present) isodiametric, ovate, peg-shaped, elliptical to rectangular; outer wall slightly thickened. Abaxial cells anticlinally elliptical or rectangular, S-shaped to polygonal; outer wall thickened, extending to radial walls in *M.* aff. *unifolia*. Stomata superficial to slightly elevated; substomatal chamber shallow but occasionally continuous with large central lacuna in *Microtis*. Mesophyll homogeneous in *Genoplesium* and *Microtis* (except *M.* aff. *unifolia* (G. Forst.) Rchb.f.); heterogeneous in other species, 1–2 palisade layers outermost (abaxial), with large interfascicular lacunae. Vascular bundles as for the tribe, in one row in *Genoplesium* or in one ring through centre of mesophyll or near adaxial surface in *Microtis* and *Prasophyllum*. Sclerenchyma bundle caps absent, except isolated fibres present abaxially on some vascular bundles in some species and abaxial caps on largest vascular bundles in *M. orbicularis* R. S. Rogers. Crystals: raphides or rod-shaped crystals in mesophyll.

Stem

TRANSECTION

Hairs absent, except unicellular and associated with mycorrhiza in *M. atrata*; occasional papillae in *M. atrata* Lindl. Cuticle thin, smooth to striate or ridged. Epidermis: cells square, anticlinally rectangular or elliptical to polygonal, often interrupted; outer wall thickened and striate, the thickenings occasionally extending to radial walls. Stomata present in some species, superficial. Cortex parenchymatous, inner layers sclerotic forming a sclerenchyma sheath. Ground tissue parenchymatous, often with large lacuna in centre. Outer or middle layers occasionally infected with hyphae and pelotons. Innermost layers of cortex in *M.* aff. *unifolia* sclerotic, forming a sclerenchyma sheath. Vascular bundles collateral, in a Y-shaped configuration, two arcs, or in one or two rings; if two rings, one often outside sclerenchyma sheath and one inside, the outer ring homologous with leaf vasculature. Xylem tracheids with helical, scalariform or pitted thickenings. Crystals: raphides and/or rod-shaped crystals in cortex or pith.

Tuber

TRANSECTION

Hairs occasional, unicellular, associated with mycorrhiza in *M. atrata*. Velamen 1–3 layered, cells elliptical to polygonal, often periclinally compressed; walls with varying thickening patterns. Outer wall of *P. cyphochilum* Benth. with scalariform wall ornamentation. Exodermis: cells isodiametric, elliptical to polygonal, walls with varying thickening patterns. Cortex parenchymatous, new tubers filled with elliptical to oblong starch grains; outer layers in old tubers dissociated; outer layers in *M. atrata* infected with hyphae and pelotons. Endodermis: cells elliptical to polygonal. Stele medullated, 2–10 arch. Dissected into five tetrarch vascular strands in *M.* aff. *unifolia*. The apparently dissected steles of *P. fimbria* Rchb.f. and *P. giganteum* Lindl. represent the fusion of 11–13 separate tubers, each with individual cortex, highly compressed with fused velamen along common boundaries. Xylem tracheids with helical, scalariform or pitted thickenings. Crystals: raphides and/or rod-shaped crystals in cortex.

Root

TRANSECTION

Hairs absent. Velamen in *Prasophyllum* and *M.* aff. *unifolia* 1–3 layered, cells elliptical to polygonal with varying wall thickening patterns. Simple epidermis (*Genoplesium*, other species of *Microtis*): cells elliptical to polygonal; outer wall thickened. Exodermis: cells elliptical to polygonal, walls uniformly thickened or outer and radial walls thickened, depending on species. Cortex parenchymatous, occasionally infected with hyphae and pelotons. Endodermis: cells elliptical to polygonal. Stele medullated, 3–8 arch. Xylem tracheids with annular, helical, scalariform or pitted thickenings. Crystals: raphides and rod-shaped crystals in cortex.

Dropper/Root-like stolon

TRANSECTION

Hairs multiseriate, associated with mycorrhiza, in some species of *Prasophyllum*; absent in *Microtis*. Epidermis: cells elliptical to polygonal, often anticlinally oriented; outer wall thickened; stomata occasionally present. Cortex parenchymatous, filled with elliptical to oblong starch grains, often infected with hyphae and pelotons. Endodermis: cells elliptical to polygonal. Stele medullated, 4–15 arch. Xylem tracheids with helical, scalariform or pitted thickenings. Crystals: raphides or rod-shaped crystals in cortex. **(AP)**

Phytochemistry

There are no phytochemical data reported in the literature for Prasophyllinae. **(NV, RG)**

Phylogenetics

Schlechter (1926) characterized Prasophyllinae by a single leaf, cauline, subulate, filiform, or narrowly linear; small flowers in a multi-flowered raceme, sometimes short, usually elongate; short column provided on each side with a more-or-less free, ring-shaped stelidium; and an anther entirely or almost free at the back. He included both *Prasophyllum* and *Microtis* within Prasophyllinae, tribe Polychondreae (= Neottieae). Soon after Mansfeld (1937) united it with Thelymitrinae, a position he maintained at a later date (Mansfeld 1954). It was Dressler and Dodson (1960), however, who reinstated Prasophyllinae, arguing that both *Microtis* and *Prasophyllum* are ‘distinctive in aspect [from *Thelymitra*], and unusual in the possession of stipes’. In subsequent treatments of the family Dressler maintained Prasophyllinae within Diurideae (Dressler 1974, 1981, 1986, 1993).

Burns-Balogh and Funk (1986*a*, *b*) interpreted Prasophyllinae as comprising a single genus *Prasophyllum*, raising it to tribal rank

Artificial key to the genera of Prasophyllinae (DJ)

1. • Flowers resupinate; column wings entire or shallowly notched, small and ear-like, flanking the anther; pollen attached directly to a viscidium via a short hamulus . . . . **50. *Microtis***
• Flowers non-resupinate; column wings large, deeply notched or with a basal lobe, erect and not flanking the anther; pollinia attached to a viscidium by a long ligulate hamulus 2

2. • Labellum immovably fixed; column foot absent; labellum with an enlarged, plate-like callus; column wings with a basal lobe; anther entire . . . . **51. *Prasophyllum***
• Labellum hinged and mobile; column foot present; labellum with a cushion-like callus; column wings deeply notched; anther with a long rostrum . . . . **49. *Genoplesium***

(although not formally) within subfamily Spiranthoideae. Szlachetko (1991) maintained Prasophyllinae as a monogeneric taxon, preferring instead to treat it as a subtribe within Diurideae, Thelymitroideae. He later transferred Prasophyllinae to his tribe Microtideae (Szlachetko 1995) by broadening the circumscription of the tribe.

Prasophyllinae have been confirmed as members of Diurideae by Clements (1995) with embryological studies and later by Clements *et al.* (in preparation) using analyses of ITS sequences of rDNA, in which *Microtis*, *Genoplesium*, and *Prasophyllum* form a distinct clade, indicating a relationship originally proposed by Schlechter (1926). **(MAC)**

49. GENOPLESIUM

Genoplesium R.Br., *Prodr.*, 319 (1810). Type species: *Genoplesium baueri* R.Br.

Prasophyllum R.Br. sect. *Bifida* G. Don, in Loudon's *Hortus Brittanicus*, 369 (1830). Type species: *Prasophyllum rufum* R.Br.

Prasophyllum R.Br. sect. *Genoplesium* Hook.f., *Fl. Tasm.*, **2**, 10 (1858). Type species: *Prasophyllum brachystachyum* Lindl.

Corunastylis Fitzg., *Austral. Orch.* **2**, back cover (Mar. 1888), *nom. illeg.*

Anticheirostylis Fitzg., *Austral. Orch.* **2** (4), back cover (Mar. 1888), *nom. illeg.*

Antichirostylis Kuntze, in Post & Kuntze, *Lex. Gen. Phan.*, 36 (1903), *orth. var.*

Prasophyllum R.Br. sect. Micranthum Rupp, *Victorian Naturalist*, **66**, 75–9 (1949), *nom. illeg.*

Derivation of name

From the Greek *genos*, race or kind, and *plesios*, near, referring to the close relationship these orchids have with *Prasophyllum*. **(DJ)**

Description (Plates 60, 61; Fig. 49.1)

Perennial geophytic *herbs*. *Roots* filamentous. *Tubers* globose to subglobose, paired, fleshy, naked; replacement tubers formed on the end of short droppers; daughter tubers absent; vertical shoots with membranous cataphylls at each node. *Leaf* single, basal, sessile; leaf of sterile plants hollow, cylindrical, longer than wide, erect, glabrous, with an obscurely developed apical lamina; leaf of fertile plants similar but solid in section, the peduncle and most of the leaf (? petiole) fused together, the apical lamina free, with involute margins. *Inflorescence* racemose or spicate, 1–many flowered, erect, terminal, developing simultaneously with the leaf; scape slender, without sterile bracts; floral bracts reduced, closely sheathing, often unequally emarginate. *Flowers* non-resupinate, dull-coloured, often with a fruity fragrance, subsessile to sessile; perianth entire or the margins adorned with cilia or hairs, the apex with an apical gland or vestigial. *Dorsal sepal* free, broader than the lateral sepals. *Lateral sepals* free or basally fused. *Petals* free, dissimilar in size, shape, and coloration to the sepals. *Labellum* free, attached by its base to the apex of the column foot, freely mobile, markedly dissimilar in shape, size, and coloration to the sepals and petals, ecalcarate; lamina not lobed, the margins entire, denticulate, erose, glandular or ciliate; callus consisting of a raised fleshy central plate, often covering most of the lamina, usually grooved, smooth, or papillate; nectar present. *Column* short; column wings fused basally to column base, erect and free distally, usually bilobed, the anterior lobe often well developed and papillate; column foot shorter than the column, ligulate, the apex erect or incurved; anther porrect, prominently rostrate; pollinia four, in two pairs, yellow, sectile, attached to a terminal viscidium via a ligulate hamulus; pollen grains in tetrads; stigma entire, quadrate, rostellum apical. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, erect, glabrous, usually ribbed; pedicels not elongated in fruit; in some species the peduncle elongates considerably in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 49.2)

A genus of about 45 species distributed in Australia, New Zealand, and New Caledonia, including Isle des Pines. **(DJ)**

Palynology

Tetrads of *Genoplesium baueri*, treated as *Prasophyllum baueri* (R.Br.) Poir. by Ackerman and Williams (1981), are similar to those of *Prasophyllum gibbosum* R.Br. (*q.v.*). **(AP)**

Ecology

Genoplesium is primarily an Australian genus with a single species, *G. calopterum* (Rchb.) D. L. Jones & M. A. Clem., from New Caledonia. Two other species, *G. pumilum* (Hook.f.) D. L. Jones & M. A. Clem. and *G. nudum* (Hook.f.) D. L. Jones & M. A. Clem., also occur in New Zealand. Within Australia *Genoplesium* is distributed from about 17° south in Queensland to about 43° south in Tasmania. In New Zealand it occurs between about 35° south and 44° south and in New Caledonia between about 20° south and 22°50′ south. These orchids are terrestrials and reproduce solely from seed, growing as individuals or widely spaced in colonies. They grow in seasonal climates and have periods of active growth and dormancy. The plants survive extremes of heat and dryness as dormant fleshy tubers partly encased in a resistant fibrous sheath, which extends to the soil surface and through which each new shoot develops. The leaves of sterile plants are hollow, but in fertile plants the leaf and flowering stem are fused and develop simultaneously as a single unit. The buds mature and flower as this fused unit elongates; in some species such as *G. nudum* substantial elongation continues prior to seed dispersal. Flowering occurs principally over summer, autumn, and winter, and seeds begin to be shed 6–12 weeks after pollination.

Species of *Genoplesium* are most abundant in coastal and near-coastal lowlands and extend to montane and subalpine regions. The genus reaches its greatest development in temperate south-eastern Australia and has few representatives within the tropics. Moss beds and accumulations of shallow soil over rock plates and rock sheets, particularly sandstone, are favoured habitats in Australia. Others

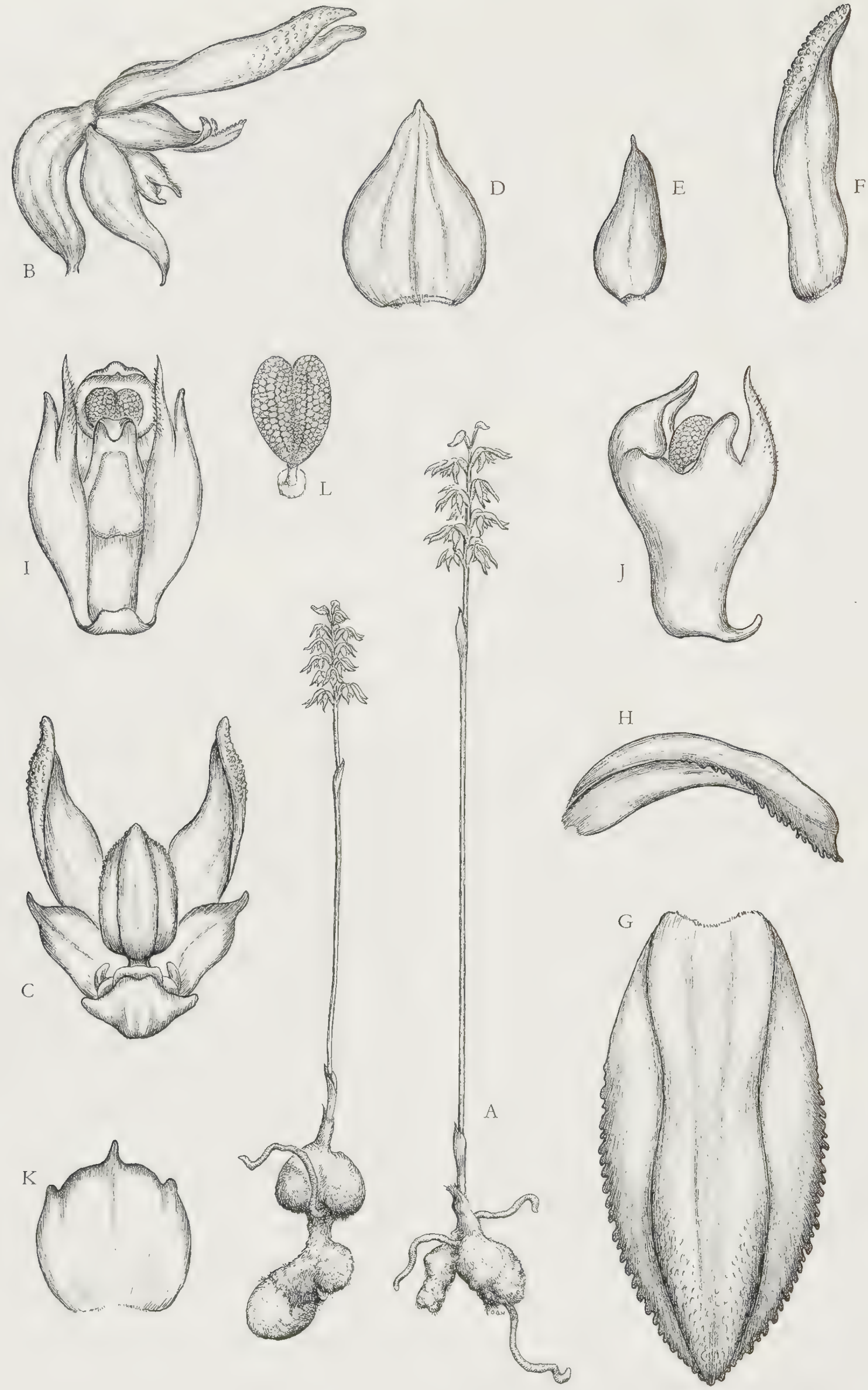

Fig. 49.1. *Genoplesium brachystachyum* (Lindl.) D. L. Jones & M. A. Clem. A. Habit, ×1; B. Flower from side, ×9; C. Flower from front, ×9; D. Dorsal sepal, ×9; E. Petal, ×9; F. Lateral sepal, ×9; G. Labellum from above, ×30; H. Labellum from side, ×21; I. Column from front, ×21; J. Column from side, ×21; K. Floral bract, ×15; L. Pollinarium. Drawn by Oliver Q. Whalley.

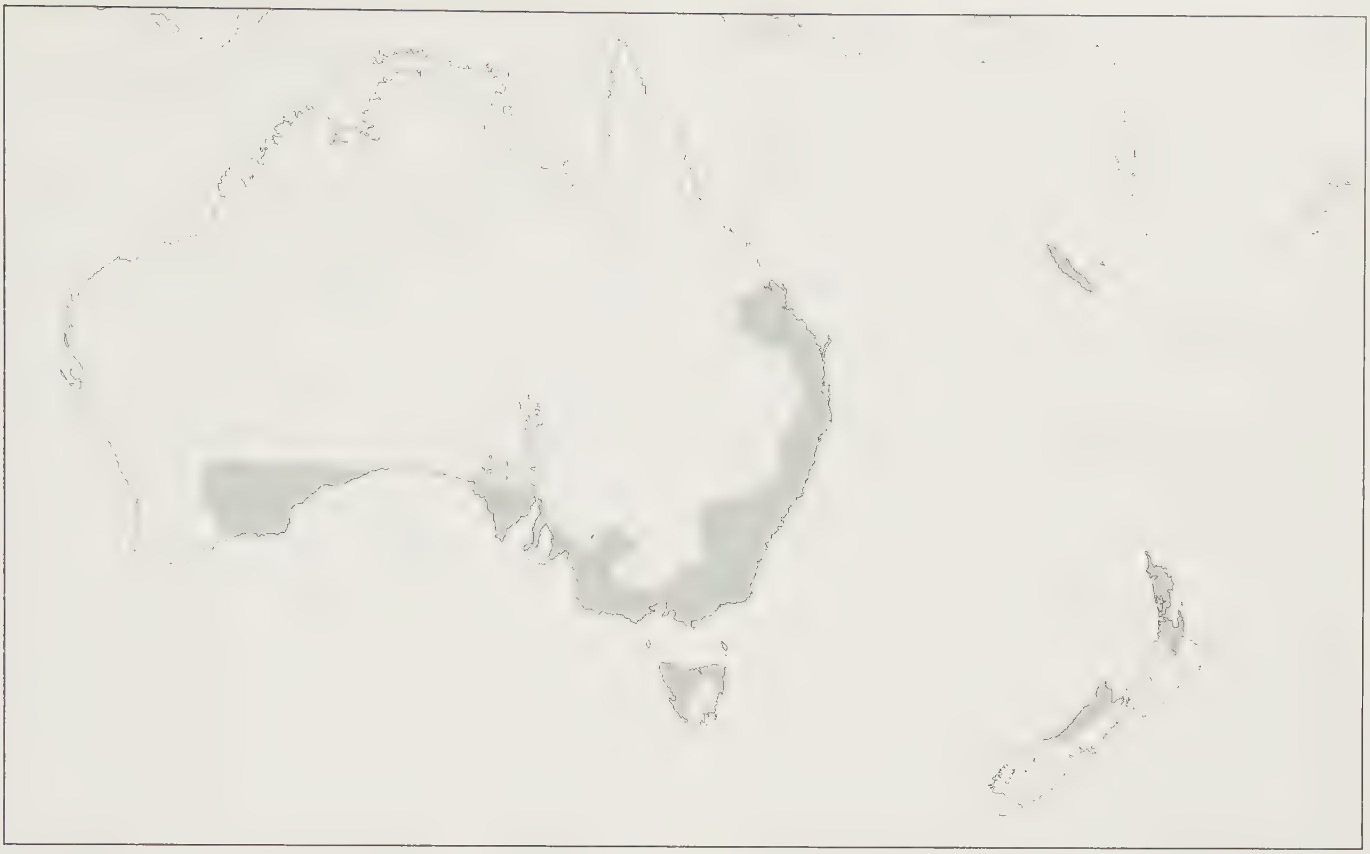

Fig. 49.2. Distribution map of *Genoplesium.*

include sclerophyll forest and woodland; montane grassy forests; heathland over sand or limestone; mallee shrubland over limestone and subalpine bogs. In New Zealand *Genoplesium* species occur in moist grassy areas, swamps, and bogs. In New Caledonia *G. calopterum* grows in stunted maquis developed on ultrabasic soils. **(DJ)**

Pollination

Formal scientific studies on the pollination of *Genoplesium* are lacking, but there have been a number of anecdotal reports by naturalists which provide some insights (Garnet 1940; Jones 1970*d*; Bates 1981*a*, 1988). The flowers of *Genoplesium* are small, inconspicuous, and dull-coloured in shades of reddish brown, purple, and green. The perianth may be fringed with cilia, the latter hanging loosely and waving freely in the breeze in some species. These characteristics conform most closely to myophily (fly pollination; van der Pijl and Dodson 1966), which is borne out by the limited data indicating that *Genoplesium* is pollinated exclusively by small, compact flies of the superfamily Chloropoidea. Garnet (1940) reported the presence of nectar in some *Genoplesium* species, indicating that the pollination strategy is one of nectar reward. A few species are autogamous (Jones 1972*a*, 1998*d*), and one is apomictic (Jones 1977; Jones and Clements 1989)

Jones (1972*b*) reported that *Genoplesium nudum* (as *Prasophyllum beaugleholei* Nicholls) and *G. pumilum* (as *P. aureoviride* Rupp) are autogamous. He also noted (Jones 1998*e*) that populations of *G. archeri* (Hook.f.) D. L. Jones & M. A. Clem. in south-west Tasmania are autogamous, whereas the species is entomogamous throughout the rest of its large range. *Genoplesium nudum* has a suite of characteristics typical of autogamous orchids (Jones 1972*b*). The flowers are short-lived, lasting only two to three days. The pollinia lack coherence, even in the bud, and are only weakly attached to the viscidium, which lacks a viscid secretion and is unlikely to be removed by an insect. Ovaries on all plants swell and contain viable seed by contrast to outcrossing species in which many ovaries do not produce seeds.

The mechanism of self-pollination in *G. nudum* is simple but does not commence until the flower has opened (Jones 1972*b*). The anther is located behind the narrow upper half of the stigma and is separated from it by the rostellum in the early bud. Two days before the flower opens the rostellum moves forward of the anther, the pollinia are incoherent, and the stigma has become moist but not sticky. After the flower opens the anther sacs split wide open, the pollinia rest on the back of the rostellum, which has bent further forward in front of the stigma to an angle of 45°or less, and pollen grains begin to fall on the now-sticky stigmatic surface. As flowering progresses pollination appears to involve two processes; the loose pollen grains crumble over the rostellum onto the stigma, and the stigma grows around the rostellum to meet them. The stigma ultimately becomes swollen and distorted.

The dominant pollination mechanism in *Genoplesium* appears to be xenogamy or geitonogamy mediated by small flies. The early observations of Garnet (1940) remain the most thorough and complete pollination study of the group so far. He studied four species near Melbourne in Victoria, although their exact identity is uncertain due to recent taxonomic revisions (Jones and Clements 1989; Jones 1991; Jones and Jeanes 1996; Jones 1998*e*). Over several seasons he observed the behaviour of flies visiting *G. morrisii* (Nicholls) D. L. Jones & M. A. Clem., *G. archeri* (but possibly *G. ciliatum* (Ewart & B. Rees) D. L. Jones & M. A. Clem.), *G. nigricans* (R.Br.) D. L. Jones & M. A. Clem. (probably an undescribed species related to *G. rufum*; Backhouse and Jeanes 1995), and *G. despectans* (Hook.f.) D. L. Jones & M. A. Clem. Other observations are those of Jones (1970*d*) on five species and Bates on *G. ciliatum* (as *Prasophyllum archeri*; Bates 1981*a*) and *G. acuminatum* (R. S. Rogers) D. L. Jones & M. A. Clem. (Bates 1988).

The attraction of flies to some *Genoplesium* species is very strong, and it is common for several to many flies to swarm over fresh inflorescences (Garnet 1940; Bates 1981*a*, 1988). Flies respond rapidly to bait flowers placed in the field. Bates (1981*a*) noted a response by seven flies within one minute of exposing a pot of *G. ciliatum* flowers. Such rapid responses are similar to those of pollinators sexually attracted by pseudo pheromones (Peakall 1990). Attraction to *Genoplesium* appears to be by odours, not all of which may be detectable by humans. Garnet (1940) could detect an odour in *G. despectans* but not *G. morrisii*, *G. archeri* or *G.* aff. *rufum*. *Genoplesium fimbriatum* has a strong lemon scent, which increases in intensity with rising temperature (Jones 1970*d*). Blaxell (1970) reported that *G. apostasioides* (as *Prasophyllum anomalum* Rupp) has a faint lemon scent, *G. archeri* smells of sour milk, *G. citriodorum* D. L. Jones & M. A. Clem. (as *P. morrisii*) has a strong lemon fragrance (see also Jones 1991), and *G. simulans* D. L. Jones (as *G. morrisii* var. *intermedium*) has a weak lemon scent mixed with an ant-like aroma, though Jones (1991) indicated *G. simulans* lacks a lemon fragrance. Blaxell detected no odour in *G. nudiscapum* (Hook.f.) D. L. Jones & M. A. Clem. (as *P. densum*), *G. pumilum* (Hook.f.) D. L. Jones & M. A. Clem. (as *P. aureoviride*) and *G. nudum* (as *P. beaugleholei*); the latter two species are autogamous, so the lack of an odour is not surprising. Although flowers of *G. acuminatum* (R. S. Rogers) D. L. Jones & M. A. Clem. were actively visited by flies, no odour could be detected (Bates 1988).

The available records of visitors to *Genoplesium* species all involve flies of the closely related families Chloropidae and Milichiidae of the superfamily Chloropoidea, indicating that *Genoplesium* is specifically adapted to these fly families as pollinators. Specimens collected by Garnet (1940) were identified as belonging to four or five species in three genera and two families, but only three were named, all chloropids, as follows: *Caviceps flavipes*, *Oscinosoma subpilosa*, and an undescribed species of *Oscinosoma*. The specific orchid species visited by each fly species were not given. A photograph in Cady and Rotherham (1970) shows a chloropid bearing pollinia on the labellum of *G. archeri* (as *Prasophyllum archeri*) and captioned as *Conioscinella becker*. The reliability of the identification cannot be assessed because no details of the observation are given in the text. The identities of the insects observed by Jones (1970*d*) and Bates (1981*a*, 1988) were not given, but the flies collected by D. L. Jones were subsequently identified by D. Colless (unpublished) as follows: species of *Caviceps* on *G. nigricans*, *G. despectans*, *G. morrisii*, and *G. rufum*; *Caviceps flavipes* was also collected on *G. rufum*. As an additional unpublished record, flies caught by A. E. Logan on *G.* aff. *rufum* at Carabost, New South Wales, were identified by D. K. McAlpine of the Australian Museum as chloropids of the genus *Lioscinella* and milichiids of the genus *Stomosis*.

The mechanism of insect-mediated pollination in *Genoplesium* was described in detail by Garnet (1940). Attracted flies landed on the inflorescence and moved to the downward-hanging labellum, which they gradually walked up, probing with their proboscis as they went. He noticed the prominent raised callus plate of the labellum appeared to exude droplets of nectar, which the flies seemed to imbibe. Once on the labellum the flies became totally absorbed and were unperturbed by close observation with a hand lens or even inversion of the flowers (Garnet 1940; Bates 1981*a*). The flies moved to the base of the labellum (Garnet 1940), forcing their way below the rostellum by jerking movements of the legs (Bates 1981*a*, 1988), where they spent up to several minutes. In this position the fly's thorax contacted the viscidium. Garnet proposed that the stout hairs on the fly's thorax punctured a thin membrane over the viscidium releasing the glue, although it is more likely the sticky viscidium simply stuck to the insect's dorsum (Plate 61). Once the pollinarium has been removed, the stipe connecting the pollinia to the viscidium bends through 90° to bring the pollinia into a position above the fly's head, where they would contact the stigma of the next flower visited.

After flies have finished on one flower they may move to others on the same raceme (Garnet 1940), raising the possibility of geitonogamous pollination. This behaviour also indicates that the flies are deriving a reward for their efforts (Bates 1988). An unusual observation by Bates was that flies responded to flowers of *G. acuminatum* taken inside a house after dark. The flies, one of which was carrying pollinia, were small enough to pass through the mesh on a screen door.

The available data do not allow definite conclusions to be made about the degree of pollinator specificity in *Genoplesium*. Garnet (1940) did not report which species of flies were attracted to each *Genoplesium* species but stated that pollinators were shared among species, allowing the possibility of hybridization. However, hybrids were not apparent in mixed populations of *Genoplesium* species that he examined. By contrast, observations by Jones (1970*d*) and Bates (1988) indicated that some level of specificity may occur. Jones observed that small flies behaved differently toward five species of potted *Genoplesium* placed together. The flies removed the pollinaria of only one species, *G. morrisii*, but also actively worked the flowers of *G. despectans*. They landed on the inflorescence of *G. fimbriatum* but did not enter the flowers and showed little interest in *G. nigricans* (as *Prasophyllum fusco-viride* Reader). The flies ignored *G. filiforme* (as *P. nublingii* R. S. Rogers) altogether. Similarly, Bates (1981*b*) observed that larger flies visited *G. ciliatum*, then went to *G. nigricans* and *G.* aff. *rufum* in the same glasshouse over the same time period. However, Bates (1988) also found that the same unidentified fly species visited *G. acuminatum* and *G. ciliatum* in the glasshouse. It should be noted that *G. acuminatum* and *G. ciliatum* do not occur sympatrically; the former is found in coastal northern New South Wales and Queensland, and the latter in southern Victoria and South Australia. It appears that allopatric *Genoplesium* taxa, which have no opportunity to hybridize, may attract the same pollinators.

Hybrids have been reported among some *Genoplesium* species, indicating that pollinator specificity is incomplete. Hybrids between *G. ciliatum* (as *Prasophyllum archeri*) and *G. despectans* (as *P. despectans*) have been reported by Bates and Weber (1979), and Backhouse and Jeanes (1995) reported that *G. archeri s.s.* also hybridizes with *G. despectans*. Jones (1991) reported that hybrids may occur between *G. citriodorum* and *G. simulans*, two closely related species in the *G. morrisii* complex, but only in disturbed sites. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Genoplesium is not widely cultivated because of limited appeal and difficulty in culture.

Mix: basic with extra drainage material such as coarse sand. Light: 50% shade. Watering: from summer to early autumn, depending on the species, until late spring. Flowering: from summer to late autumn. Propagation: best propagated from seed sown around parent plants. **(HR)**

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50. MICROTIS

Microtis R.Br., *Prodr.*, 320 (1810). Type species: *Microtis rara* R. Br.

Goadbyella R. S. Rogers, *Trans. & Proc. Roy. Soc. South Australia* **51**, 294 (1927). Type species: *Goadbyella gracilis* R. S. Rogers.

Derivation of name

From the Greek *mikros*, small, and *ous*, *otos*, ear, in reference to the small column wings that subtend the anther. **(DJ)**

Description (Plates 62, 63; Fig. 50.1)

Perennial geophytic *herbs*. *Roots* filamentous. *Tubers* globose to subglobose, paired, fleshy, naked; replacement tubers formed on the end of short droppers; daughter tubers formed on the end of slender root-like stolons; vertical shoots with membranous cataphylls at each node. *Leaf* single, basal, sessile; lamina much longer than wide, erect, cylindrical, terete, hollow, glabrous. *Inflorescence* racemose or spicate, few–many flowered, erect, terminal, emergent through a membranous point on the upper part of the leaf; scape wiry, without sterile bracts; floral bracts reduced, closely sheathing. *Flowers* resupinate, green, subsessile to sessile. *Dorsal sepal* free, much broader than the lateral sepals, cucullate over the column. *Lateral sepals* free, often recurved. *Petals* free, smaller than the sepals. *Labellum* free, attached by its base to the anterior column base, markedly dissimilar in shape, size and coloration to the sepals and petals, ecalcarate; lamina not lobed, the margins entire or with irregular clusters of callus cells, the apex entire, emarginate or notched; callus consisting of a raised fleshy basal plate which is sometimes lobed or notched, often with an accessory apical granular callus, rarely the callus entirely absent; nectar present. *Column* short; column wings fused basally to column, erect and free distally, the free parts closely subtending the anther; column foot absent; anther erect, parallel to the axis of the column, rostrate or not; pollinia four, yellow, granular, attached via a short hamulus to a dorsal viscidium; stigma entire, quadrate; rostellum apical. *Ovary* elongate, ribbed, glabrous, swelling rapidly during anthesis. *Capsules* dehiscent, erect, glabrous; pedicels not elongated in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 50.2)

A genus of about 18 species distributed in Australia, New Zealand (including Stewart Island and Chatham Island), Indonesia, Malaysia, Philippines, Japan, Taiwan, and China. **(DJ)**

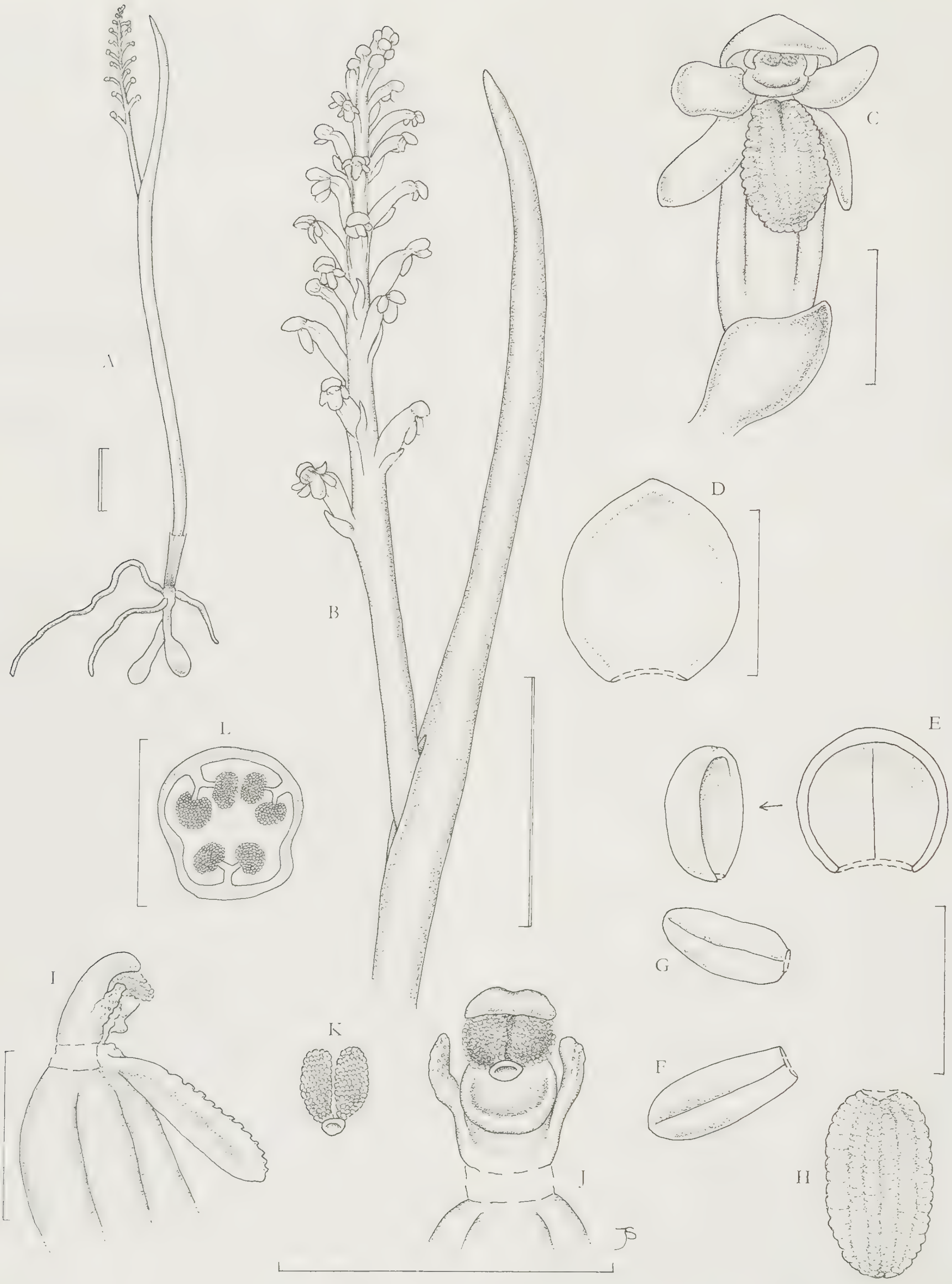

Fig. 50.1. *Microtis atrata* Lindl. A. Habit; B. Inflorescence; C. Flower; D. Bract; E. Dorsal sepal; F. Lateral sepal; G. Petal; H. Labellum; I. Labellum and column, side view; J. Column, front view; K. Pollinarium (showing two of four pollinia); L. Ovary, transverse section. Single bar = 1 mm; double bar = 1 cm. Drawn by Judi Stone from *Morrison s.n.* (K) and Kew Spirit Collection no. 53219.

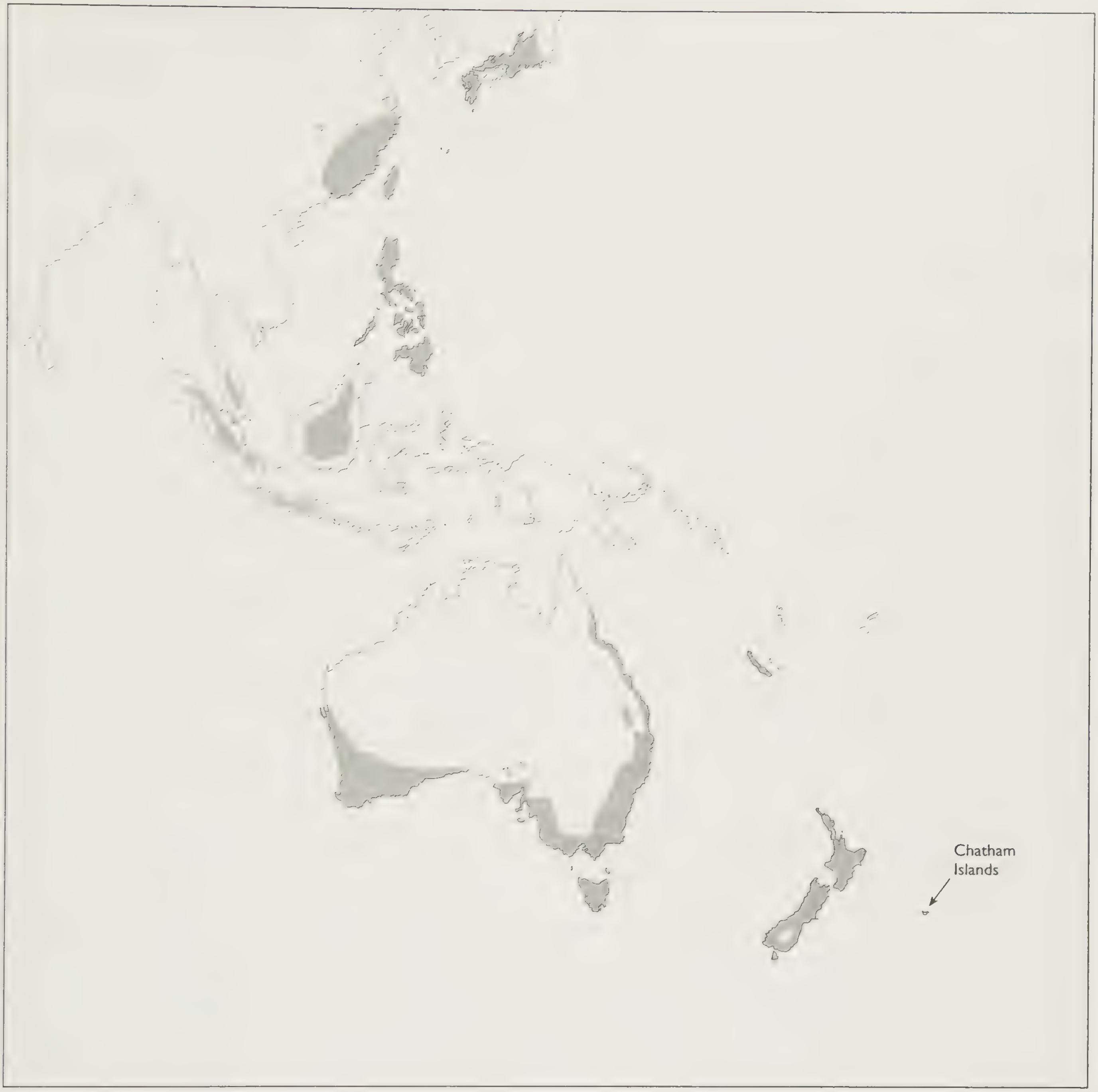

Fig. 50.2. Distribution map of *Microtis*.

Palynology

Tetrads of *Microtis unifolia* are rhomboidal, *c.* 29 μm; inaperturate; semitectate; and reticulate (Ackerman and Williams 1981). **(AP)**

Ecology

Microtis has a wide latitudinal distribution, occurring from about 36° north in Japan to about 47° south on Stewart Island. All species are terrestrial, distributed from coastal lowlands to montane and subalpine zones, occupying temperate, subtropical, and highland tropical regions. The greatest concentration and diversity within *Microtis* occurs in Australia and to a lesser extent New Zealand. Within Australia *Microtis* ranges between about 15°30′ south near Cooktown in Queensland to about 43° south in Tasmania. In New Zealand it occurs between about 35° south and 47° south. In general these orchids favour moist to wet habitats. Common habitats in Australia include grassland and grassy forests, mesic sites in sclerophyll forest and woodland, heathland, mallee shrubland over limestone, and subalpine grassy meadows and herbfields. Two species, *M. atrata* and *M. orbicularis*, grow in moist to wet swamps, usually with the plants partially or nearly fully submerged. New Zealand species of *Microtis* occur in swamps, bogs, moist grassy areas, and montane and alpine herbfields. In Malesia and Asia *Microtis* species mainly occur on mountain tops in stunted scrub or among grass.

These orchids reproduce from seed and also form local clonal colonies by the production of daughter tubers on the end of root-like stolons. All species, including those within the tropics, grow in areas with a seasonal climate. The plants have distinct growth and dormancy phases, surviving extremes of heat and dryness as small fleshy tubers. The leaves of *Microtis* are fully expanded prior to flowering, and the developing inflorescence grows up the centre of the hollow leaf and breaks through at a weak point just prior to flowering.

Flowering occurs principally over spring and summer, and the seeds begin dispersing 6–12 weeks after pollination. Flowering in some species of *Microtis* is greatly stimulated by summer fires, and a few species, such as *M. pulchella* R.Br., have become strictly dependent on the intervention of fires to induce flowering. In others the response is less dramatic.

Microtis seeds germinate readily, and seedlings can flower within one or two years after germination. Some highly adaptable species, such as *M. parviflora* R.Br. and *M. unifolia*, can quickly colonize new sites, especially areas of disturbance, and also persist in altered regimes such as lawns and pastures. **(DJ)**

Pollination

There have been few studies on the pollination strategies of *Microtis*. The small pale green, yellowish or whitish flowers are borne in an inconspicuous grass-like raceme and do not seem to conform to any previously defined pollination syndrome for orchids (van der Pijl and Dodson 1966) or indeed other plants (Peakall *et al.* 1991; Proctor *et al.* 1996). The available evidence indicates that *Microtis* is adapted for pollination by microhymenoptera, particularly small wingless ants, but also tiny winged parasitic wasps. The pollination mechanism in insect-pollinated species is nectar reward, at least in *Microtis parviflora* R.Br. (Jones 1975; Peakall and Beattie 1989). Some species are facultatively self-pollinating, and some are said to be apomictic (Bates 1984*d*; Jones 1988; Bates and Weber 1990).

Only two detailed studies of insect pollination have been conducted, both on *Microtis parviflora*, a widespread and variable species (Jones 1975; Peakall and Beattie 1989). These studies found *M. parviflora* is primarily pollinated by several species of small wingless worker ants. The dominant pollinators in both studies were species of *Iridomyrmex*—an unidentified species near Melbourne (Jones 1975) and *I. gracilis* near Sydney (Peakall and Beattie 1989). Other ant species bearing pollinia were a species of *Meranoplus* and *Rhytidoponera tasmaniensis* (Jones 1975), and species of *Monomorium*, *Crematogaster*, and *Polyrachis* (Peakall and Beattie 1989). Bates (1981*b*) found that small wasps (Ichneumonidae and Braconidae) were the only insects to pick up *Microtis* pollinia in a putative hybrid swarm of *M. oblonga* R. S. Rogers (as *M. rara* R.Br.), *M. unifolia*, and *M. parviflora* near Mylor in South Australia.

Many other insects may visit inflorescences for the nectar but do not pick up pollinaria and may be regarded as nectar thieves. These include many small flies, particularly mycetophilids (Jones 1975), and beetles (Peakall and Beattie 1989; Bates and Weber 1990). A beetle observed by Peakall and Beattie removed pollinaria on its proboscis and legs but did not move between inflorescences.

Pollinators are attracted by the presence of nectar in the case of *M. parviflora* (Jones 1975; Peakall and Beattie 1989) and probably other species, though there are no other specific references to nectar. Thomson (1879) assumed the pit between the basal glands of *M. unifolia* was a nectary but could find no evidence of nectar. Similarly Bates (1981*b*) stated there was no nectar in three species of *Microtis* flowers near Adelaide in South Australia. The failure to find nectar may relate to the time of day when observations were made. It is likely that nectar accumulated overnight is largely removed from flowers in the morning, and this accords with the pattern of ant activity observed by Peakall and Beattie (1989) (see below). Lack of nectar may also relate to the onset of autogamy in the older flowers of facultatively autogamous species.

Some *Microtis* species emit sweet fragrances, which are likely to be an added attraction for pollinators. These are described as weak in *M. parviflora* (Jones 1975; Peakall and Beattie 1989) but are stronger in other species. A sweet scent like that of *Boronia megastigma* (Rutaceae) occurs in *M. oblonga* (as *M. rara* in Bates 1981*b*; Jones 1988 and *M. oblonga* in Backhouse and Jeanes 1995). A strong musky (Jones 1988) or sweet (Hoffman and Brown 1992) odour is associated with *M. alba*. Odours are more likely to attract flying insects from a distance than flightless ants, which probably encounter food sources mainly by active searching and direct contact.

Jones (1975) found ants actively foraging on flowers of *M. parviflora* up to three days old, whereas older flowers were examined briefly or ignored. Peakall and Beattie (1989) observed that ants foraged only on newly opened flowers beginning at about 07:30 but with most activity between 08:30 and 11:30. Jones noted that ants were most active between 18 and 26°C but ceased activity above 32°C. On hot days a burst of activity would occur in the late afternoon as the temperature fell.

Visiting ants would climb onto the labellum lamina and probe briefly along it until they reached a pool of nectar in a depression between the bilobed basal labellum callus and the foot of the column. Here they would feed for up to six minutes (Jones 1975; Peakall and Beattie 1989). In *Iridomyrmex* and the other small ant species, movements of the head during feeding brought the viscidium on the overhanging rostellum into contact with the frons just above the mandibles (Plate 63). Larger individuals of *Rhytidoponera* contacted the viscidium with their jaws. The pollinarium was removed as the ant retreated. The presence of the pollinarium on the smaller ants did not seem to disturb them, but *Rhytidoponera* was able to scrape the pollinarium from its jaws onto the inflorescence. Some ants carried up to four pollinaria (Jones 1975; Peakall and Beattie 1989).

Similar feeding movements at other flowers pressed the pollinia into the stigma where a layer of pollen was removed and spread over the sticky surface; occasionally a whole pollinium was deposited (Jones 1975; Peakall and Beattie 1989). A single pollinarium could pollinate many flowers as usually only a small portion was left on each stigma. Peakall and Beattie observed pollinaria to remain intact for up to 50 flower visits. Individual ants spent up to ten minutes on an inflorescence and visited up to five inflorescences, often repeatedly. *Iridomyrmex gracilis* carried pollinaria between plants for distances from 1–76 cm with a mean of 6.2 cm. Ants performed many geitonogamous pollen transfers, but a significant amount of outcrossing also occurred (Jones 1975; Peakall and Beattie 1989).

Ant pollination in *Microtis parviflora* achieved high percentages of swollen seed capsules, a mean of 96.6% in the Sydney population, with pollinaria removed from 85.9% of flowers (Peakall and Beattie 1989). Similar high levels of pollinaria removals and pollination occurred in Melbourne populations (Jones 1975). At one site 97.2% of flowers were pollinated, and 86% had their pollinaria removed; at another the respective figures were 66.6% and 64.0%.

Ant pollination in orchids and other plants is rare (Beattie 1985; Peakall *et al.* 1991; Peakall 1994); the only fully documented cases of ant pollination showing transfer of viable pollinia between plants are for three orchid species (Peakall *et al.* 1991). The rarity of ant pollination is thought to relate mainly to the presence on the cuticle of antibiotic secretions from the metapleural glands (Peakall *et al.* 1991). These secretions, as well as protecting ants from pathogenic micro-organisms, are toxic to most types of pollen. However, tests of the toxicity of the cuticle of *Iridomyrmex gracilis* to the pollen of *Microtis parviflora* and *Brassica rapa* showed *I. gracilis* does not have secretions of a type or quantity to disrupt pollen function. An additional factor of importance in orchids is that orchid pollen is usually not directly exposed to the vector's cuticle. In the case of *M. parviflora* the pollinia are held free of the ant's body by a stipe (Peakall and Beattie 1989).

Species of small wasps in the families Ichneumonidae and Braconidae were found to be abundant visitors to flowers of *M. oblonga*, *M. unifolia*, and *M. parviflora* near Adelaide in South Australia (Bates 1981*b*). The ichneumonid visitors comprised all males, whereas those of the braconid were both males and females. The wasps were active on hot afternoons and could be seen on about 20% of inflorescences at any one time. Early in the flowering season up to half the wasps carried pollinaria. Incoming wasps would land on the inflorescence, move to the vertical labellum and walk upward to the base where they would place their heads between the large basal calli. In this position the viscidium of the pollinarium contacted the wasp's head. According to Bates the pollinia fall or rotate forward on the stipe after the wasp withdraws, thereby positioning them at the front of the head where they will contact the stigma of other flowers.

Tests on the mating system of the Sydney population of *M. parviflora* showed that flowers were self-compatible and that autogamy did not occur (Peakall and Beattie 1989). By contrast, similar tests on Melbourne populations showed *M. parviflora* was facultatively autogamous but not apomictic (Jones 1975). Field experiments by R. Bates suggested apomixis may occur in *M. orbicularis* (Bates 1983*a*) and some forms of *M. unifolia* (Bates 1984*d*). However, M. A. Clements (unpublished) has been unable to find apomictic ovules in any *Microtis* taxa in detailed embryological studies.

On the other hand, autogamy has been well documented in several *Microtis* species. Thomson (1879) described the process in *M. unifolia* (as *M. porrifolia* (Sw.) R.Br. ex Spreng.) in New Zealand. He found *M. unifolia* to be facultatively autogamous; it has a functional pollinarium that can be removed easily by an insect, but the species also self-pollinates. On one inflorescence with 32 open flowers, all but the most recently opened one had the pollinaria removed. However, if the pollinarium was not removed, as may happen commonly in some seasons, most flowers self-pollinated. Some time after anthesis the pollinia became withered and brown and were partially pulled from the anther. The pollen grains germinated and a 'great mass of tubes' penetrated the upper margin of the stigma. Other New Zealand species reported to be predominantly self-pollinating are *M. oligantha* and *M. parviflora* (Molloy 1990).

Jones (1975) reported a slightly different mechanism of autogamy in *M. parviflora*. During the first three days after anthesis the upper margin of the stigma gradually grew upward around the edge of the rostellum and over the viscidium. At the same time the pollinia began to lose coherence. About four days after anthesis the margin of the stigma met the pollinia, resulting in fertilization. A similar process occurs in *M. unifolia* (Bates 1984*d*) with the pollinia being contacted by the upward-growing stigma from two to seven days after anthesis, depending on the population. The pollen tubes grow through the top, front, and rear of the stigma. Once self-fertilization commences the nectaries dry, and insects are no longer attracted. It has been claimed that autogamy is likely to occur in most *Microtis* species because nearly all flowers seem to develop mature seed capsules, with the exception of those injured or diseased (Bates 1984*d*). However, this claim needs to be balanced against the fact that at least some populations of *M. parviflora* are not autogamous but still have high levels of entomogamous pollination (Peakall and Beattie 1989). These high levels of fertilization are probably a consequence of the nectar reward provided to pollinators and contrast with the often low levels of capsule development common in deceptive species.

Hybrids are not often reported in *Microtis*, indicating that effective barriers to hybridization are usually present in nature (Bates 1984*d*). Two hybrids were documented by Bates; *M. alba* × *M. media* (as *M. unifolia*) and *M. unifolia* × *M. oblonga* (as *M. rara*). The former is now regarded as a species in its own right, *M.* aff. *alba* (Hoffman and Brown 1992). The remaining hybrid involves two taxa in the *M. unifolia* complex, which seems to include all suspected hybrids so far identified (Bates 1984*d*). Backhouse and Jeanes (1995) also showed that hybrids may occur among *M. unifolia* and its near relatives, *M. arenaria* Lindl. and *M. oblonga* in Victoria. Bates (1981*b*, 1984*d*) suggested hybrids in the *M. unifolia* complex are 'quite fertile', resulting in the formation of hybrid swarms. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Many species are easy to cultivate, but they are not the most popular because of their small, green, insignificant flowers. The most attractive species, such as *M. alba* R.Br., are more difficult to maintain. *Microtis* seed germinates readily in almost any medium, so it is advisable to remove developing seed pods before they dehisce.

Mix: basic. Light: 50% shade. Watering: autumn to late spring or early summer. Many *Microtis* species grow in wetter areas, so in cultivation they respond well to standing the pot in a vessel containing 1–2 cm of water. Flowering: during spring and into summer. Those in cultivation flower well. Propagation: the species in cultivation, e.g. *M. unifolia*, *M. parviflora*, are colony-formers (average multiplication ×2). **(HR)**

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51. PRASOPHYLLUM

Prasophyllum R.Br., *Prodr.* 317 (1810). Type species: *Prasophyllum australe* R.Br.

Derivation of name

From the Greek *prason*, leek, and *phyllon*, leaf, in reference to the leaves of these orchids, which resemble onions or leeks. **(DJ)**

Description (Plates 64, 65; Fig. 51.1)

Perennial geophytic *herbs*. *Roots* filamentous. *Tubers* globose to subglobose, paired, fleshy, naked; replacement tubers formed on the end of short droppers; daughter tubers usually absent, rarely formed on the end of root-like stolons; vertical shoots with membranous cataphylls at each node. *Leaf* single, basal, sessile; lamina much longer than wide, erect, cylindrical, terete, hollow, glabrous. *Inflorescence* racemose or spicate, few–many flowered, erect, terminal, emergent through a membranous point on the upper part of the leaf; scape wiry to stout, sometimes flexuose, without sterile bracts; floral bracts reduced, closely sheathing. *Flowers* non-resupinate, dull-coloured, often sweetly fragrant, subsessile to sessile. *Dorsal sepal* free, broader than the lateral sepals. *Lateral sepals* free or variously connate. *Petals* free, usually dissimilar in size, shape, and coloration to the sepals. *Labellum* free, rigidly attached by its base or by a short immobile claw to the anterior column base, markedly dissimilar in shape, size, and coloration to the sepals and petals, ecalcarate; lamina not lobed, often strongly recurved near the middle, sometimes papillate, the margins usually undulate to crispate, rarely subentire; callus consisting of a raised fleshy central plate, usually channelled and often ridged, smooth, rugose or papillate, the base expanded into a broad shallow basin; nectar present. *Column* short, nearly as long as wide; column wings fused basally to column base, erect and free distally, usually with a small basal posterior lobe; column foot absent; anther basifixed, erect and parallel to the axis of the column, rostrate; pollinia four, in two pairs, yellow, sectile, attached to a terminal viscidium via a ligulate hamulus; pollen grains in tetrads; stigma entire, quadrate, rostellum apical. *Ovary* usually not much longer than wide, sometimes elongate, ribbed, glabrous. *Capsules* dehiscent, erect, glabrous, usually ribbed; pedicels not elongated in fruit. Seeds numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 51.2)

A genus of about 80 species distributed in Australia and New Zealand, including Stewart Island and Chatham Island. **(DJ)**

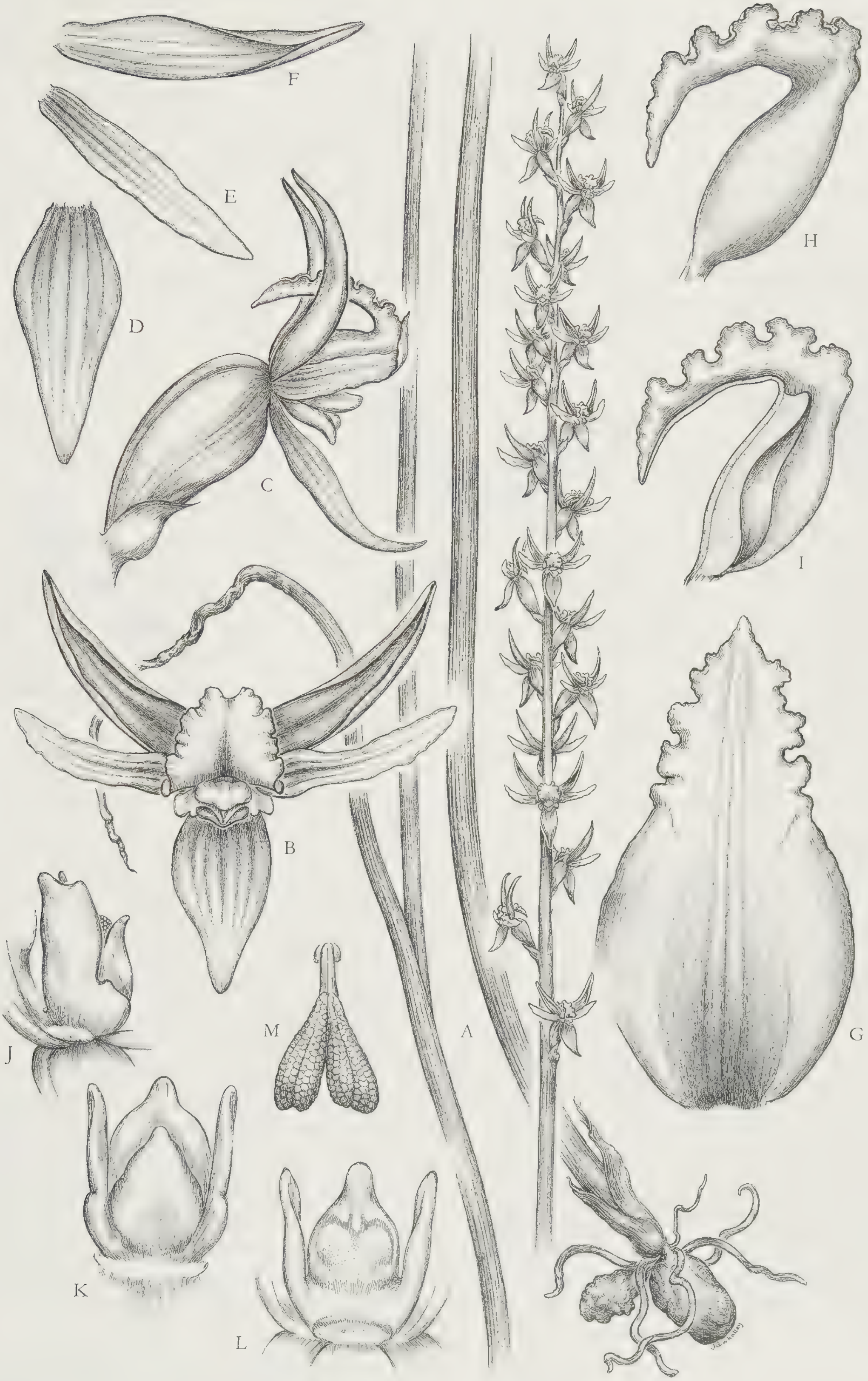

Fig. 51.1. *Prasophyllum robustum* (Nicholls) M. A. Clem. & D. L. Jones. A. Habit, ×1; B. Flower from front, ×1; C. Flower from side, ×4.5; D. Dorsal sepal, ×4.5; E. Petal, ×4.5; F Lateral sepal, ×4.5; G. Labellum flattened, from above, ×9; H. Labellum from side, ×9; I. Labellum, longitudinal section, ×9; J. Column from side, ×9; K. Column from below, ×9; L. Column from above, ×9; M. Pollinarium, ×9. Drawn by Oliver Q. Whalley.

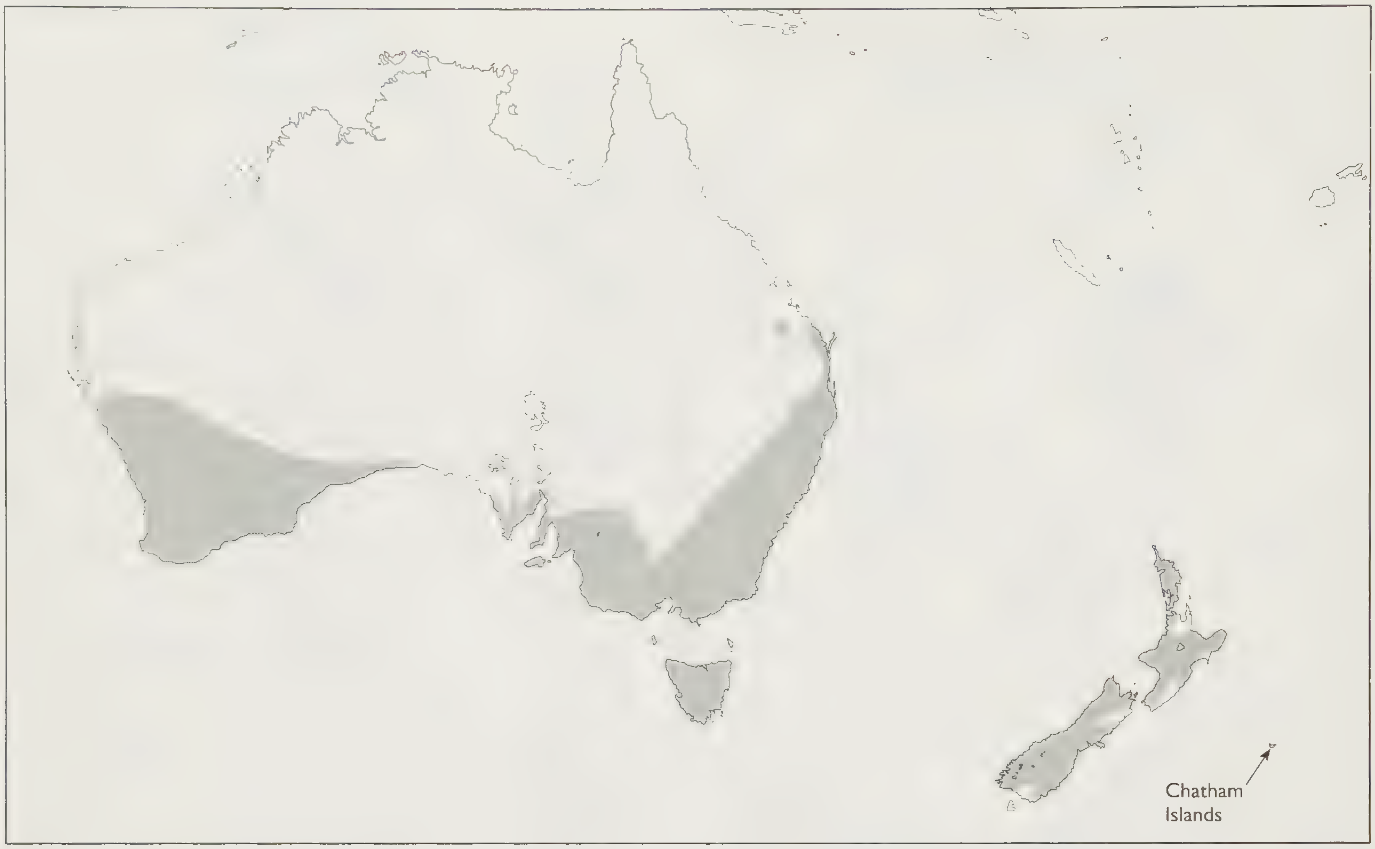

Fig. 51.2. Distribution map of *Prasophyllum.*

Infrageneric treatment

Three sections have been described within *Prasophyllum*, but they have limited application in view of the complexity of this genus which requires revisionary studies. **(DJ)**

Prasophyllum section **Integra** G. Don, in Loudon's *Hortus Brittanicus*, 369 (1830). Type species: *Prasophyllum elatum* R.Br.

Prasophyllum section **Prasophyllum** (= **Euprasophyllum** Hook.f., *Fl. Tasm.*, **2**, 9 (1858), *nom. illeg.*)

Prasophyllum section **Podochilus** Benth., *Fl. Aust.*, **6**, 335 (1873). Type species: *P. striatum* R.Br.

Palynology

Tetrads of *Prasophyllum gibbosum* R.Br. are *c.* 50 μm, tetrahedral; inaperturate; semitectate; rugulate-baculate to irregularly suprabaculate; the units globose-spherical (Ackerman and Williams 1981). **(AP)**

Ecology

Prasophyllum is essentially an Australian genus with all but two or three species endemic there, the others occurring in New Zealand. In Australia the genus is distributed between about 24°30′ south in Queensland and 43° south in Tasmania. In New Zealand it occurs between about 30° south on the North Island and about 47° south on Stewart Island. All species are terrestrials, and most reproduce solely from seed, the plants occurring as individuals or in loose groups or sparse colonies. A few Australian species reproduce vegetatively by the production of extra replacement tubers to form clonal tufts; a distinctive Australian group forms clonal colonies on the end of stolonoid roots. In *P. australe* the root-like stolons are relatively short and the colonies compact; however, in *P. regium* R. S. Rogers and *P. giganteum* Lindl., they may extend for more than two metres, resulting in widely spaced plants. All species grow in areas with a seasonal climate, and the plants have distinct periods of active growth and dormancy. They avoid the extremes of summer heat, low humidity, and dryness as small fleshy tubers. *Prasophyllum* leaves are fully expanded prior to flowering. The developing inflorescence grows up the centre of the hollow leaf and breaks through at a weak point just prior to flowering. Flowering occurs mainly over spring and summer with three species flowering in the autumn. Seeds begin to be dispersed 8–12 weeks after pollination.

Species of *Prasophyllum* occur mainly in temperate regions and are distributed from coastal lowlands to montane and alpine zones, with *P. tadgellianum* R. S. Rogers occurring up to about 1650 m. They tend to favour grassy or shrubby habitats, often in moisture-retentive soils. Habitats in Australia include grassland and grassy forests, slopes, and ridges in sclerophyll forest and woodland, coastal scrub on consolidated dunes, heathland and sandplain vegetation over sand, mallee shrubland, and heathland over limestone, moist to wet swamps, particularly in subalpine regions and subalpine grassy meadows, herbfields, and feldmark. In New Zealand they occur in swamps, bogs, and alpine herbfields.

Flowering in most species of *Prasophyllum* is stimulated by summer fires, and a few species have become strictly dependent on the intervention of fires to induce flowering. Frequently species with this requirement respond in a spectacular manner, flowering *en masse* during the first season after the burn, but the numbers of flowering plants decline rapidly thereafter. Those plants growing in burned vegetation are commonly heavily pigmentated with black, perhaps to mask them from herbivores. **(DJ)**

Pollination

Pollination of *Prasophyllum* has been the subject of a number of modern studies (Jones 1972*a*; Bates 1984*e*; Bernhardt and Burns-Balogh 1986*b*; Peakall 1987, 1989*a*), and a general picture of its pollination strategies has emerged. Available data indicate *Prasophyllum* is pollinated primarily by generalized nectar-seeking insects, particularly various kinds of wasps and bees, but also flies and beetles. Visiting insects are provided with a reward of nectar, making *Prasophyllum* one of the few 'honest' genera of Diurideae. The presence of a reward encourages insects to revisit *Prasophyllum* flowers, so insect activity on plants is greater than for groups employing deceptive pollination mechanisms. Like many rewarding genera, *Prasophyllum* has racemes of multiple brightly coloured flowers, and most species emit a strong sweet odour. A few species are reported to be autogamous, and apomixis is suspected in a few others (Bates 1984*a,e*; Jones 1998*f*).

Several authors (Jones 1972*a*; Bates 1984*e*; Bernhardt and Burns-Balogh 1986*b*) have suggested that particular species of *Prasophyllum* have a single primary or dominant pollinator or group of pollinators and one or more secondary pollinators. However, most studies have been conducted at only one site or geographical area over limited time periods and do not take account of likely differences in pollinator distribution and abundance between areas and seasons. Peakall (1987) showed that two distantly related groups of insects were important pollinators of *P. fimbria* Rchb.f. and suggested the main determinants of pollinator suitability are their size and behaviour in relation to the orchid. A disadvantage of the generalized flower shape of *Prasophyllum* is that many insects unable to effect pollination visit and steal nectar (Bernhardt and Burns-Balogh 1986*b*; Peakall 1987).

Significant pollinators observed on *Prasophyllum* have included wasps, bees, and syrphid flies. Wasps from several families have been recorded removing pollinaria from *Prasophyllum* flowers: an ichneumonid, *Pterocormus promissorius*, on *P. tadgellianum* (as *P. alpinum* R.Br.; Jones 1972*a*); ichneumonids and thynnines on *P. australe*, *P. constrictum* R. S. Rogers (as *P. fuscum* R.Br.), *P. frenchii* F. Muell. (as *P. hartii* R. S. Rogers), *P. occidentale* R. S. Rogers, *P.* aff. *patens* (as *P. patens* R.Br.) and *P. validum* R. S. Rogers (Bates 1984*e*); scoliids, *Campsomeris* spp. on *P. fimbria* (Peakall 1987); and a sphecid on *P. plumaeforme* Fitzg. (as *P. ovale* Lindl. var. *triglochin* Rchb.f.; Peakall 1987). David L. Jones (unpublished) collected and formally identified male thynnine wasps removing pollinaria on their heads from *P. spicatum* R. J. Bates & D. L. Jones and *P. elatum*.

Bees of two families are also prominent: colletids on *P. elatum* (Bates 1984*e*), *P.* aff. *odoratum* (as *P. odoratum* R. S. Rogers) (*Leioproctus*, two species) (Bernhardt and Burns-Balogh 1986*b*; D. L. Jones, unpublished), *P. fimbria* (*Leioproctus*, four species), and *P. plumaeforme* (as *P. ovale* var. *triglochin*) (*Leioproctus* sp.) (Peakall 1987); and halictids on *P. fimbria* (Peakall 1987), *P. alpestre* D. L. Jones (D. L. Jones, unpublished), and *P. odoratum* (*Lasioglossum* sp.) (D. L. Jones, unpublished). Four species of hover flies (Syrphidae) commonly removed pollinaria from *P.* aff. *odoratum* (Bernhardt and Burns-Balogh 1986*b*).

Various species of beetles have been observed carrying pollinaria of *Prasophyllum* but do not appear to be significant pollinators. Rogers (1913) saw pollinaria on the thorax of several *Trogoderma adelaidae* (Dermestidae) in such a position that cross-pollination of *P. constrictum* R. S. Rogers could be effected. Coleman (1933*a*, 1934) recorded pollination of *P. drummondii* Rchb.f. by a chrysomelid beetle (*Ametalla spinolae*), and *P. australe* by rove beetles (Staphylinidae), whereas Bates (1984*e*) noted that only one beetle out of 42 seen visiting *P. elatum* bore pollinaria. Other potential pollinators observed removing pollinaria, but only in small numbers, are a megachilid bee, *Chalicodoma* sp., and an argid wasp on *P. fimbria* (Peakall 1987). David L. Jones (unpublished) has observed male and female hanging flies, *Harpobittacus australis* (Mecoptera: Bittacidae), pick up pollinaria of *P. spicatum* and *P. elatum* on their mouthparts. He has also captured syrphid flies, *Melanostoma* sp. with the pollinaria of *P. elatum* on their faces.

Domestic bees, *Apis mellifera*, may be frequent visitors to *Prasophyllum* flowers but are not regarded as important pollinators (Jones 1972*a*; Peakall 1987). Jones (1972*a*) saw a single *A. mellifera* pick up a pollinarium of *P. tadgellianum* on its mouth parts. Peakall (1987) observed only two domestic bees in over one hundred pick up pollinaria of *P. fimbria* in positions on their bodies where other flowers could be effectively pollinated.

Small and large insects incapable of effecting pollination also frequent *Prasophyllum* flowers. These include bees, wasps, beetles, ants, and flies (Jones 1972*a*; Bates 1984*e*; Bernhardt and Burns-Balogh 1986*b*; Peakall 1987). Small flies occasionally become stuck on the stigma of *P. fimbria* (Peakall 1987) and may interfere with pollen deposition, a disadvantage of the generalized pollination mechanism. Tiny flies that rest and/or feed on the flowers of *P.* aff. *odoratum* often contact the viscid disc, which adheres to the thorax (Bernhardt and Burns-Balogh 1986*b*). The pollinarium is almost as large as the insect, which cannot fly with its burden and dies in the flower. Some self-pollination may occur in this case, due to the pollinia being dragged over the stigma (Bernhardt and Burns-Balogh 1986*b*).

It is not uncommon to find pollinaria deposited on the petals or sepals of *Prasophyllum* species, indicating that some of the larger insects are able to groom them from their bodies. Coleman (1933*a*) suggested that pollinaria attached to various parts of *P. elatum* flowers were transferred from insects before the viscid discs had set. Workers of an ant, *Myrmecia* sp., which commonly fed on *P. tadgellianum*, picked up pollinaria on their large jaws but usually wiped them off onto various parts of the plant (Jones 1972*a*). Bernhardt and Burns-Balogh (1986*b*) found a large number of pollinaria on the perianth, ovaries, and leaves of *P.* aff. *odoratum* and suspected they were transferred accidentally from the probosces of syrphids as they probed the surface of the plant. It seems more likely that the pollinaria were actively wiped off by annoyed insects. Peakall (1987) observed bees and wasps attempting to remove pollinaria and noted they may fall from insects if insecurely attached, which can occur when several other pollinaria have already been collected.

Insects are attracted to *Prasophyllum* by a sweet odour, which is strong in some species, and by the dense raceme of colourful flowers. Jones (1972*a*) noted that wasps, *Pterocormus promissorius*, attracted to *P. tadgellianum* flew upwind to the flowers as if following an odour trail. The flowers of *P. tadgellianum* are inconspicuously coloured and blend in with surrounding grasses, so visual attraction from a distance is likely to be poor. However, when *P. tadgellianum* grows in groups wasps fly from raceme to raceme, apparently using short range visual cues. Peakall (1987) observed upwind flight by pollinators to *P. fimbria*. However, on any given raceme over a quarter of all flowers visited by bees and wasps were revisited by the same individual, but always for a shorter time. Second and third revisits were also occasionally observed. Previously worked racemes were also revisited, the insect landing on the same flowers as before. There were no obvious differences in visual stimulus or nectar availability between favoured flowers and the others, leading Peakall to conclude they were probably more highly perfumed.

Thynnine wasps attracted to *P. elatum* usually arrived from downwind (Bates 1984*e*), consistent with following an odour trail. *Prasophyllum elatum* has tall racemes of relatively large whitish flowers which may facilitate visual orientation. Bates suggested that *P. elatum* may mimic the flower stem of *Xanthorrhoea* spp. (Xanthorrhoeaceae), as both flower profusely after fires, often occur together, and have similarly shaped inflorescences, although those of *P. elatum* are smaller. However, a vague general similarity between two species is insufficient evidence to sustain an argument for mimicry. If mimicry is involved in *P. elatum* it can only be floral mutualism, as no deceit is involved; both species provide rewards for pollinators (Little 1983).

As would be expected, insect activity at *Prasophyllum* flowers is usually greater in the middle of the day and in warmer weather. Jones (1972*a*) noted increases in pollinator activity associated with rising temperature, which also caused increases in odour emission by *P. tadgellianum*. Thynnine wasps on *P. elatum* showed little activity on cloudy days or at temperatures below 20°C. They were most active above 25°C and were still working at 35°C, whereas natives bees were also more active above 20°C (Bates 1984*e*). Colletid bees visited *P.* aff. *odoratum* on warm, clear days between 11:00 and 14:00, but syrphid flies also foraged in cooler conditions between 09:00 and mid-afternoon, even on cool, cloudy days or in light rain (Bernhardt and Burns-Balogh 1986b). Peakall (1987) found pollinator activity on *P. fimbria* was confined to sunny periods between 11:30 and 14:30 when temperatures were above 16°C. However, domestic bees, *A. mellifera*, were active on *P. fimbria* from early morning to late afternoon, even on cool overcast days. Pollinator activity on *P. fimbria* corresponded to the period of peak nectar production by the flowers with little nectar being produced overnight.

Nectar is secreted on the lower part of the labellum callus plate, forming a pool between the perianth parts at the top of the ovary. In some species beads of nectar are exuded on the outer parts of the callus plate, forming a trail into the flower (Coleman 1933*a*). Most insects simply drink the nectar, but Bates (1984*e*) stated that thynnine wasps punctured the surface of the callus plate to release additional supplies.

Upon arrival at the flowers most insects position themselves head downward on the reversed labellum (Plate 65), but some may utilize the dorsal sepal in a head-up position. The petals block the sides of the flower and ensure correct orientation of the pollinator (Coleman 1933*a*). The upturned sides of the basal half of the labellum form a U-shaped channel, which also serves to align the pollinator along the labellum. The column appendages may also assist in orienting the head of the insect in relation to the rostellum and stigma. When insects imbibe nectar at the base of the labellum the front of the head is pushed into the stigma of the short column and contacts the viscidium, which adheres to the top of the frons of appropriately sized wasps and bees. On large insects, such as beetles, the pollinarium may attach to the labrum or jaws.

On *P. tadgellianum*, the wasp *Pterocormus promissorius* adopted the head-up position and probed along the labellum picking up pollinaria on its mouthparts and below the head. Thynnine wasps on *P. elatum* (Bates 1984*e*) and syrphids on *P. aff. odoratum* (Bernhardt and Burns-Balogh 1986*b*) consistently probed the base of the labellum in the head-down position and usually collected pollinaria on the facial region (frons). Native bees (Bernhardt and Burns-Balogh 1986*b*; Peakall 1987) and scoliid wasps (Peakall 1987) adopted either position, sometimes using both orientations on the same raceme (Peakall 1987).

Some insects, generally smaller bees (Bates 1984*e*) and syrphids (Bernhardt and Burns-Balogh 1986*b*), carried only one pollinarium, but larger wasps and some bees carried multiple pollinaria (Bates 1984*e*; Bernhardt and Burns-Balogh 1986*b*; Peakall 1987). Bees captured on *P.* aff. *odoratum* had up to five pollinaria (Bernhardt and Burns-Balogh 1986*b*), whereas those on *P. fimbria* carried an average of 5.25 pollinaria (maximum of 10); one specimen had at least 23 viscidia, most with the pollinia removed (Peakall 1987). Scoliid wasps on *P. fimbria* carried an average of 3.7 pollinaria (Peakall 1987).

Insects spend relatively long periods drinking nectar in flowers with plentiful supplies. This may allow time for the viscid disc to set before the insect retreats. Coleman (1933*a*) observed that if a needle is used to rupture the outer membrane of a viscid disc but is quickly withdrawn, the disc does not adhere. If, however, the needle is left for a short period the disc sticks and is removed on the needle. Jones (1972*a*) reported that wasps spent 'quite a time' feeding at each flower of *P. tadgellianum*. Bates (1984*e*) observed that thynnine wasps on *P. elatum* might spend up to a minute on some flowers but only one or two seconds on others. This may depend on the amount of nectar available, which in turn may be a function of the age of the flower or whether it has been pollinated or recently visited. Peakall (1987) recorded feeding intervals by insects of 5–30 seconds with most lasting 10–20 seconds on *P. fimbria*.

There is some confusion in the literature regarding rotation of the stipe and pollinia after their removal from the anther. Rogers (1913) stated that the pollinia of *P. constrictum* rotate through an angle of 180°after they are removed. Coleman (1933*a*) also noted rotation of pollinia in *P.* aff. *odoratum*, stating that it is swift and spring-like. These observations are difficult to explain as there appears to be little need for rotation of pollinia in *Prasophyllum*; they are already in a good position to contact the stigma of another flower when pulled from the anther, which is directly behind the stigma. Bates (1984*e*) noted that the pollinia of *P. elatum* simply fall forward over the face of the insect under their own weight.

There is also confusion concerning the role of 'sprung' pollinia. Several authors have noted that if pollinia are not removed by an insect they may be pulled or 'sprung' from the anthers to be suspended by the stipe from the rostellum (Rogers 1913; Coleman 1933*a*; Bernhardt and Burns-Balogh 1986*b*). Rogers considered this resulted from a peeling back of the anther point to expose the pollinia, followed by drying and curling of the stipe, which pulls the pollinia free. Cady and Rotherham (1970) suggested that springing was caused by forward movement of the rostellum, which pulled the pollinia from the anther. Curling of the stipes then brings the pollinia into a 'prominent position to be attached to any interfering insect'. Rogers was the first to suggest that springing of pollinia preceded removal by insects. This is unlikely to be the case as the curled stipe places the pollinia in a poor position to contact the stigma of another flower. Springing of pollinia appears to confer no advantage and may be a peculiarity of overmature flowers.

In only a small percentage of pollinations in *Prasophyllum* is a whole pollinarium transferred to a stigma. Jones (1972*a*) found that only 15% of pollinated flowers of *P. tadgellianum* received a complete pollinarium. In most flowers a small to large portion of the pollen is deposited allowing each pollinarium to fertilize several flowers. A similar situation occurs in *P.* aff. *odoratum* (Bernhardt and Burns-Balogh 1986*b*) and *P. fimbria* (Peakall 1987, 1989*a*). By labelling pollinia with coloured dyes, Peakall (1987, 1989*a*) demonstrated that flowers of *P. fimbria* frequently receive pollen from more than one source. For example, 44% of flowers receiving labelled pollen also had unlabelled pollen on their stigmas. Peakall (1987, 1989*a*) found an average of two flowers were pollinated for each pollinarium removed, with a maximum of almost seven pollinations per removed pollinarium at one site.

Jones (1972*a*) and Peakall (1987) examined experimentally the effects on seed set and flower senescence of partial versus full deposition of pollinia on the stigma. Jones noted that most ovaries of *P. tadgellianum* swell to a considerable extent after the flower opens, giving the impression they will set seed, even if they had not been fertilized. However, by about three weeks after flowering, fertilized ovaries appear shiny, swollen, and turgid, whereas sterile ones are dull and less swollen. Fertilized ovaries are firm when squeezed, but sterile ones flatten and feel empty. To test this hypothesis, Jones pollinated flowers with whole pollinaria or by brushing a pollinarium over the stigma, using either pollen from the same flower (self-pollination) or a different plant (cross-pollination). Control plants were unpollinated with or without removing their pollinia from the anther. The control plants failed to develop seed, showing that *P. tadgellianum* is not autogamous or apomictic. Both self-pollinated and cross-pollinated flowers produced equal amounts of seed, demonstrating self-compatibility. Ovaries fertilized by whole pollinaria produced twice as much seed as ovaries receiving part of a pollinarium.

Peakall (1987) obtained similar results for *P. fimbria* and extended them with additional experiments. He found that seed viability and pollen tube growth were similar for selfed and cross-pollinated flowers. However, there were differences in the behaviour of flowers pollinated with either excess pollen over the whole stigma or pollination covering less than a quarter of its surface. Fully pollinated flowers closed within 48 hours, and the ovaries had swollen noticeably by eight days. Partially pollinated flowers remained open at 2.5 days and secreted nectar normally; the first flowers closed at 5 days and the last by 17 days. Unpollinated flowers remained open for at least 10 days. Delayed closure of partially pollinated flowers retains the opportunity for additional pollination to maximize seed set and increase the chances of cross-pollination, thereby broadening genetic variation in the seed.

Pollination percentages reported for *Prasophyllum* vary from quite low to fairly high. Coleman (1933*a*) estimated overall pollinaria removals in *Prasophyllum* were of the order of 70–80%, and about 40% of stigmas were pollinated. Jones (1972*a*) reported that 80% of *P. tadgellianum* flowers had their pollinaria removed, with 77% being pollinated. Seed capsules were produced by 52% of flowers in populations of *P.* aff. *odoratum* studied by Bernhardt and Burns-Balogh (1986*b*). Seven populations of *P. fimbria* examined by Peakall (1987) had pollination percentages between 30% and 78% with all but one over 50%. The low percentage at one site appeared to be related to competition for pollinators from profusely flowering vegetation in a nearby unburnt area.

Prasophyllum fimbria, like many other *Prasophyllum* species, undergoes enhanced flowering after bushfires. The advantage appears to be that insects are forced to forage on the few fire-stimulated plants, such as *Prasophyllum*, thereby enhancing the chances of pollination (Peakall 1987). The fact that many flowers on each raceme open simultaneously and that pollinators may visit several of these before moving to another plant indicate there is considerable potential for geitonogamous pollen transfer. The degree of outcrossing versus self-pollination in *P. fimbria* depends partly on pollinator behaviour. Insects initially landed on any part of a raceme, possibly the most attractively perfumed flower. Subsequent movement on the raceme was highly variable; some insects moved only upward or downward from flower to flower, whereas others moved both up and down. Many flowers were missed, either because insects moved directly to flowers above or below, ignoring the spiral arrangement of flowers around the rachis or because they walked or flew past a set of flowers without probing them, despite the fact that many contained nectar. This behaviour differs from the systematic foraging considered optimal on inflorescences with a uniform nectar distribution, in which it is expected that each flower would be visited in stereotyped up, down or spiral movements beginning at the top or bottom of the inflorescence (Peakall 1987). The observed behaviour may be related to differential attractiveness between flowers and reduces the amount of self-pollination.

The distribution of labelled pollen on inflorescences of *P. fimbria* studied by Peakall agreed with that expected from pollinator foraging patterns. Similar variable behaviour of pollinators appears to occur on other *Prasophyllum* species. Jones (1972*a*) noted that *Pterocormus promissorius* landed on the lowest flowers of *P. tadgellianum* and worked up the raceme in a spiral fashion, but the wasps examined only a few flowers in detail. Bates (1984*e*) stated that thynnine wasps on *P. elatum* might feed on up to a dozen flowers or only one before flying to the next raceme. Syrphids on *P.* aff. *odoratum* rarely visited more than three or four flowers per raceme, whereas colletid bees tended to land in the middle of the inflorescence and move spirally between flowers (Bernhardt and Burns-Balogh 1986*b*). Bees were more likely to effect self-pollination than syrphids as the former tended to visit more flowers on the raceme.

Monitoring of pollen movement between flowers within and between inflorescences of *P. fimbria* using pollinia marked with coloured dyes showed that the proportion of geitonogamous transfers varied from 4–57% with a mean of 22.2% across five sites (Peakall 1989*a*). Forty percent of flowers received both labelled and unlabelled pollen. It was estimated that the proportion of flowers receiving some xenogamous pollen approached 85.5%. The heterogeneity of pollen transferred was increased by pollinators gaining loads of pollinaria and flowers receiving multiple visits from vectors. In addition pollinators were found to transfer pollen between flower spikes over a mean distance of 8 m and up to 28 m. Peakall (1987) conducted genetic analyses on *P. fimbria* and found that, despite the apparent potential for significant self-pollination, gene frequencies did not differ from those expected for an outcrossing species.

There is little information on autogamy or apomixy in *Prasophyllum*, and that presented is fragmentary and confused. The best evidence for autogamy is from the sole New Zealand species, *P. colensoi* Hook.f. (Thomson 1879; Molloy 1990). Thomson found the pollinia were incoherent and that pollen grains germinated through the back and top of the stigma from the anther, which is located behind. However, he also noted the flowers had a sweet scent and, although they appeared to lack nectar, showed some evidence of insect visitation. Four flowers out of 75 on nine racemes had partially removed pollinia, but even in these self-pollination had commenced. It is possible that *P. colensoi* is facultatively autogamous.

Although several Australian species, *P. gracile* (Rogers 1913), *P. goldsackii* J. Weber & R. J. Bates, *P. constrictum* (as *P. fuscum*), *P. fitzgeraldii* R. S. Rogers & Maiden, and *P. pallidum* Nicholls (Bates 1978*c*) were said to be self-pollinating, little concrete evidence was presented. Bates (1984*a*, *e*) put forward a different view of these species, stating most were actually apomictic. Only *P. pallidum* is self-pollinating according to Bates (1984*a*, *e*), whereas *P. goldsackii*, *P. calcicola* R. J. Bates (as *P.* aff. *macrostachyum*), *P.* aff. *fitzgeraldii* (now *P. fecundum* R. J. Bates) and *P.* aff. *fuscum* R.Br. were said to be apomictic or partly apomictic, but no data were provided. A carefully controlled scientific study is needed to sort out the confusion surrounding these taxa.

The mechanism of self-pollination described by Rogers (1913) in *Prasophyllum gracile* (actually *P. constrictum* R. S. Rogers) is unique. He observed that pollinia 'sprung' from the anthers could be rotated, by the action of the stipe as it aged, from behind the stigma to above the rostellum, and finally down onto the centre of the stigma. Throughout this process the viscidium remained in its slot in the rostellum above the stigma. If the pollinia deviated to one side the lateral appendages of the column directed the pollinia onto the stigma. *Prasophyllum constrictum* is an outcrossing species, so this form of autogamy is facultative. However, the process observed by Rogers (1913) appears to be atypical; Bates (1981*c*) indicated he was unable to find further examples. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Members of this large genus are not widely cultivated probably because many appear difficult to maintain for long periods and also because they are not widely available.

Mix: basic. Light: 50% shade. Watering: autumn to late spring. Flowering: species flower from late autumn to early summer. Many species in the wild require a hot summer fire to flower. Some species in cultivation will flower regularly. Propagation: most are solitary species, and limited experience has shown that tuber removal is successful. Otherwise seed should be sprinkled around parent plants. **(HR)**

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SUBTRIBE RHIZANTHELLINAE

Rhizanthellinae R. S. Rogers, *J. Roy. Soc. West Australia*, **15**, 4 (1928). Type species: *Rhizanthella gardneri* R. S. Rogers.

Description

Glabrous, mostly subterranean, holomycotrophic, geophytic *herbs*. *Rhizomes* perennial, thickened, branching laterally, with or without tubers. *Roots* absent. *Leaves* reduced to colourless fleshy scale leaves. *Inflorescence* a condensed, many-flowered capitulum surrounded by enlarged imbricate bracts. *Flowers* non-resupinate, spirally arranged, inward-facing, dull-coloured, sessile; tepals dissimilar, partially fused and forming a short curved tube open on the anterior side. *Labellum* hinged to the apex of the column foot; lamina unlobed, fleshy; nectar absent. *Column* with a foot present, pollinarium present; pollinia four. *Fruit* an indehiscent berry. **(DJ)**

Phylogenetics

Since its description the affinities of Rhizanthellinae have been much debated, the taxon having been variously placed in the Gastrodieae (Rogers 1928), a position to which Lavarack (1971, 1976) and Dressler (1981) have both subscribed based on the possession of mealy pollen, partial fusion of the perianth segments and a mycoparasitic habit. Dressler and Dodson (1960), in their reassessment of the phylogeny of the family, suggested that the form of the labellum, column, and anther of Rhizanthellinae indicated an alliance with *Caladenia* rather than with Gastrodieae and placed the subtribe in Neottieae with Chloraeinae, Cryptostylidinae, Diuridinae, Limordinae, Neottiinae, Prasophyllinae, Pterostylidinae, and Spiranthinae. Dressler (1986) placed Rhizanthellinae within Diurideae without comment, which is where it remained in his subsequent treatment of the family (Dressler 1993).

Balogh (1982) likened the *Rhizanthella* to the Northern hemisphere genus *Cephalanthera* (Epidendroideae) on the basis of putative similarities of column, anther, and pollen morphology and reduced Rhizanthellinae to a synonym within Limodorinae, tribe Neottieae. This position was based on results of a phylogenetic analysis of the family (Burns-Balogh and Funk 1986*a*, *b*). Clements and Cribb (1984) referred *Rhizanthella* to Diurideae on the basis of floral morphology. Garay (1986) preferred, however, to include Rhizanthellinae in subfamily Neottioideae (tribe Vanilleae) based on possession of *Vanilla*-type sclerotic seeds and fleshy, indehiscent, aromatic fruits with parietal placentation.

Szlachetko (1991), in his radical treatment of Diurideae as the new subfamily Thelymitroideae, failed to account for Rhizanthellinae. In his system of classification of the family he preferred to treat Rhizanthellinae as an isolated tribe, Rhizanthelleae, within his subfamily Thelymitroideae (Szlachetko 1995).

Despite the unusual plant habit and floral morphology of the two described species in Rhizanthellinae, their inclusion within Diurideae was confirmed when it was discovered they possess a diurid-type embryo (Clements 1995). Additional molecular studies (Kores *et al.* 2000; Cameron and Chase, 2000; Clements *et al.*, in preparation) confirm that Rhizanthellinae is part of Diurideae. **(MAC)**

52. RHIZANTHELLA

Rhizanthella R. S. Rogers, *J. Roy. Soc. West. Australia*, **15**, 1 (1928). Type species: *Rhizanthella gardneri* R. S. Rogers.

Cryptanthemis Rupp, *Proc. Linn. Soc. New South Wales*, **57**, 58 (1932). Type species: *Cryptanthemis slateri* Rupp.

Derivation of name

From the Greek *rhiza*, root, *anthos*, flower, and the diminutive suffix *-ella*, small, referring to the direct attachment between the rhizomes and the inflorescence. **(DJ)**

Description (Plates 66, 67; Fig. 52.1)

Perennial, mostly subterranean, holomycotrophic *herbs*. *Stems* fleshy, subterranean, persistent, horizontal to vertical, producing new shoots at intervals from nodes; horizontal and vertical shoots with colourless fleshy cataphylls at each node. *Roots* absent. *Root tubers* absent. *Stem tubers* formed at the end of short, relatively slender stems. *Leaves* absent, reduced to sheathing, appressed scale leaves; lamina mostly ovate-lanceolate, fleshy, convolute in bud, margins entire; venation anastomosing. *Inflorescence* capitulate, many-flowered, erect, terminal, held at or just below ground level; capitulum bracts enlarged, imbricate, spirally arranged in one or two rows, enclosing, surrounding or subtending the capitulum, pigmented with anthocyanins; floral bracts elongate, erect, fleshy, each closely

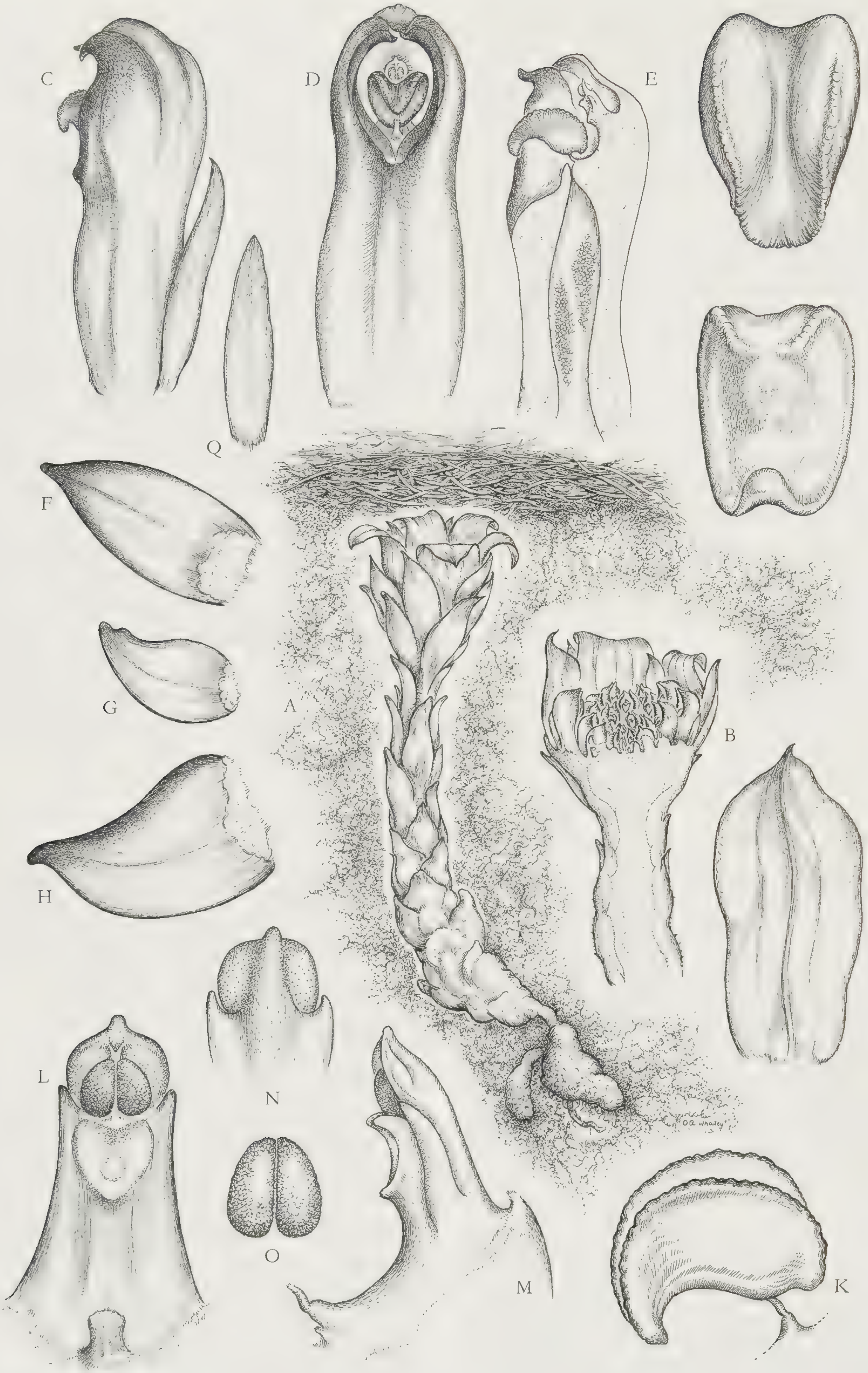

Fig. 52.1. *Rhizanthella gardneri* R. S. Rogers. A. Underground habit, ×1; B. Inflorescence, ×1.5; C. Flower from side, ×9; D. Flower from front, ×9; E. Flower (including ovary), longitudinal section, ×9; F. Dorsal sepal, ×9; G. Petal, ×9; H. Lateral sepal, ×9; I. Labellum from above, ×21; J. Labellum from below, ×21; K. Labellum from side, ×21; L. Column from front, ×21; M. Column from side, ×21; N. Column apex from back, ×21; O. Pollinia, ×36. Drawn by Oliver Q. Whalley from Kew Spirit Collection nos. 45300 and 46628.

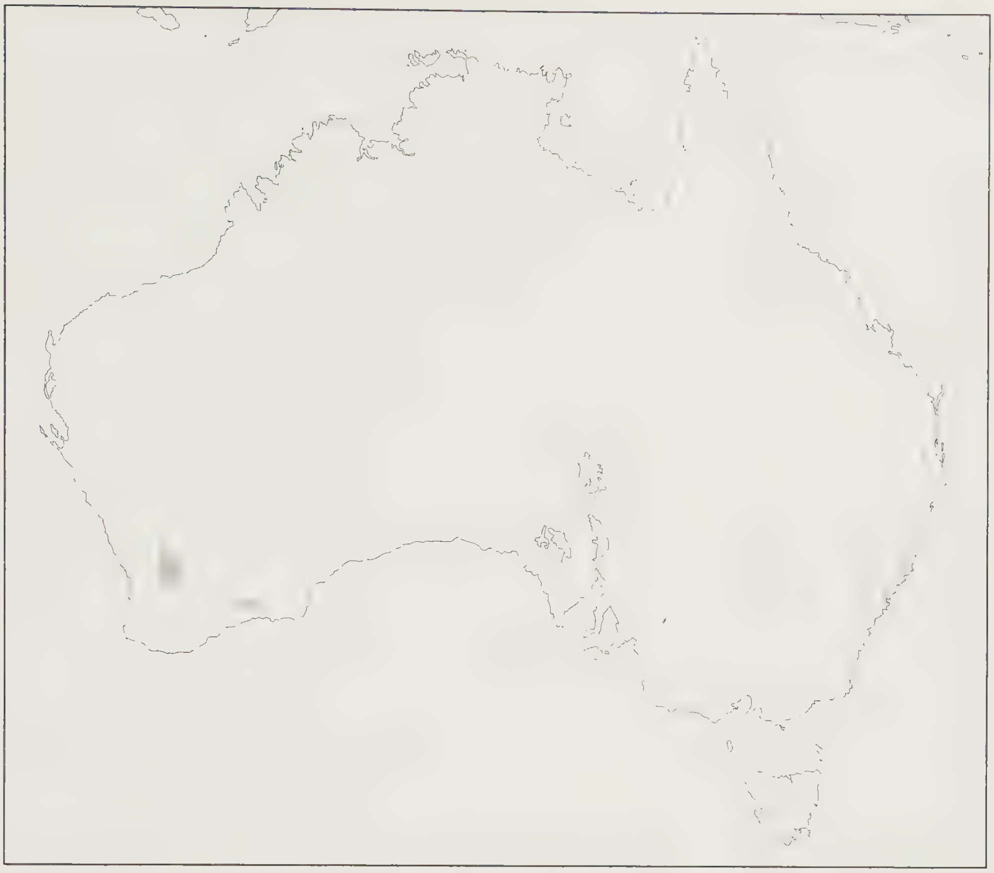

Fig. 52.2. Distribution map of *Rhizanthella.*

subtending a flower. *Flowers* non-resupinate, spirally arranged, inward-facing, dull-coloured, sessile. *Sepals* and *petals* papillate, forming a short, curved, hood-like tube open on the anterior side. *Dorsal sepal* fused basally to the lateral sepals, cucullate. *Lateral sepals* fused basally to the dorsal sepal and each other, erect. *Petals* fused basally to the column, smaller than the sepals. *Labellum* free, hinged by a narrow basal claw to the apex of the column foot, markedly dissimilar in size, shape, and coloration to the sepals and petals, ecalcarate; lamina not lobed, thick and fleshy, papillate, conduplicate; callus obscure; nectar absent. *Column* short; wings mostly fused to the column, distally free, irregular, papillate; column foot vestigial, anther terminal, four-celled, persistent, basifixed, erect, papillate, non-rostrate; pollinarium consisting of two pollinia attached directly to a viscidium; pollinia clavate, granular, yellow; viscidium terminal; rostellum apical; stigma entire, circular, concave. *Ovary* elongate, glabrous, not ribbed. *Berry* indehiscent, fleshy, globoid, glabrous, erect, yellowish to reddish; sepals and petals persistent; peduncle not elongating in fruit. *Seeds* 50–150 per fruit, cream to blackish, sculptured, not winged. **(DJ)**

Distribution (Fig. 52.2)

A genus of two species endemic in Australia; one species occurs in Western Australia, the other in New South Wales and southern Queensland. **(DJ)**

Anatomy

Tuber (stem)

TRANSECTION

Hairs absent. Cuticle thick, heavily suberized, smooth. Epidermis: cells elliptical to polygonal, outer wall slightly thickened. Stomata absent. Ground tissue parenchymatous, cells with relatively thick walls and large nuclei, some cells infected with pelotons. Vascular bundles collateral, in one ring. Xylem tracheids with helical or scalariform thickenings. Ergastic substances: none observed. **(AP)**

Palynology

Nothing has been published about the pollen ultrastructure of *Rhizanthella.* **(AP)**

Phytochemistry

There are no phytochemical data reported in the literature for *Rhizanthella.* **(NV, RG)**

Ecology

These remarkable plants are commonly known as 'underground orchids' because their entire existence, including flowering, is subterranean. The tips of the floral bracts may emerge above the litter layer, but the flowers usually remain covered. The plants themselves are leafless and throughout most of the year consist of an entire or branched, fleshy, colourless rhizome with fleshy bract-like cataphylls toward the apex.

Rhizanthella gardneri from Western Australia has a narrow distribution in two widely disjunct areas, roughly between about 31°30′ south and 33°45′ south, restricted to a winter-rainfall belt of 300–400 mm annually. It grows with a *Rhizoctonia*-like endophyte and a mallee variant of the myrtaceous shrub *Melaleuca uncinata* R.Br. (commonly called broombush), the orchid plants usually occurring within 30 cm of a living *Melaleuca* plant. The dominant surrounding vegetation is mainly mallee shrubland or mallee heath.

Flowering occurs between May and July with the flowering heads terminating a vertical shoot. They develop just beneath the soil surface, which may crack open, although the flower heads remain covered by the broombush litter. Little is known of the seed dispersal mechanism, but mature fruits are fleshy and may be ingested by small herbivores with the result that the relatively large hard seeds of the orchid pass through in the dung.

Rhizanthella slateri (Rupp) M. A. Clem. & P. J. Cribb from eastern Australia is distributed between about 33° south and 35° south in New South Wales with a disjunct record from south-eastern Queensland at about 28°15′ south. It grows in sclerophyll forest and woodland dominated by various myrtaceous trees and shrubs, particularly *Eucalyptus* spp. and *Melaleuca* spp., but also *Tristaniopsis laurina* (J. J. Sm.) P. G. Wilson & J. T. Waterhouse and *Syncarpia glomulifera* Niedenzu, all in Myrtaceae. Flowering occurs in October and November. Collections of this latter species have been mainly accidental, although in recent years some success has been achieved after systematic searching. **(DJ)**

Pollination

The great rarity of *Rhizanthella* and its hidden subterranean inflorescences make the study of its pollination difficult. For a long time the cryptic habit of *Rhizanthella* species led to speculation they were self-pollinated (Dressler 1981). However, Rupp (1934) could find no evidence of it in *R. slateri*, and few flowers of *R. gardneri* matured seed (George and Cooke 1981), indicating that it is not self-pollinating. Visual cues for potential pollinators are virtually nil, so olfactory stimuli are the most likely mode of attraction. In warm weather, a faint sweet fragrance is given off and seems the most probable enticement for potential pollen vectors. However, when cut, plants emit a pungent odour similar to formalin (George 1980; George and Cooke 1981). *Rhizanthella* species provide no food for pollinators (D. L. Jones, unpublished), although Clements and Cribb (1984) speculated that visitors are probably seeking food. It seems likely that *Rhizanthella* is a food-deceptive species, but more work is needed to prove this hypothesis.

The thick, pale flower stem of *Rhizanthella* grows upward to just below the soil surface from the tip or lateral shoot of a fleshy underground rhizome. The spirally arranged flowers are clustered tightly in a dense, concave, daisy-like head within broad fleshy bracts. The flowers face inward and open sequentially from the outside inward over a period of a week or so per inflorescence. In the case of *R. gardneri* the expanding bracts around the flower head push up the sandy soil surface into a slight mound with small cracks, up to a centimetre wide, allowing entry by pollinators (George 1980; George and Cooke 1981). The bracts create an air space above the concave capitulum and occasionally straighten to protrude through the soil surface. The flowers are always 1.0–1.5 cm below ground. The pressure of the bracts on the soil is such that if the covering layer is removed the bracts open outward, completely exposing the flowers.

Insects observed carrying pollinaria include a single small fly, *Megaselia* sp. (Phoridae; George and Cooke 1981), and tiny wasps and termites (Dixon 1985). The *Megaselia* was only 2 mm long and carried the pollinarium on the rear of its dorsal thorax. Members of its family are associated with and breed in dead organic matter. Termites, being flightless, are unlikely to effect significant cross-pollination but could effect pollination among flowers on the same inflorescence. Pollinaria were attached to the heads of the termites (Dixon 1985).

The mechanism of pollinaria removal has not been observed. The column is enclosed by a shroud-like hood formed by the adnate tepals (illustrated in Clements and Cribb 1984). Access by pollinators is via a narrow orifice between the lateral sepals, through which the tiny labellum protrudes, as shown by Nicholls (1969) and Clements and Cribb (1984). The labellum of both *Rhizanthella* species is mobile and, according to Dixon (1985), that of *R. gardneri* is once or twice irritable, indicating insects may be propelled against the column. It appears that insects attracted to flowers generally climb onto the labellum and are tipped against the column as they move toward the base past the point of balance. The viscidium adheres to the head or thorax of the insect, and the pollinia are pulled free as it retreats. The pollinia are attached directly to the viscidium (Clements and Cribb 1984).

Observations by Dixon (1982) showed that less than 25% of flowers developed viable seed under natural conditions. However, if plants were partially exposed for several weeks by removing some of the soil cover, seed set increased to over 80%, equivalent to that achieved by artificial pollination. Thus, exposing the plant provides easier access for pollinators or access to a greater variety of potential pollinators. The advantages of greater exposure of flowers appear to be outweighed by natural selection for subterranean flowering, which may be related to mechanisms of seed dispersal.

Seed development in *R. gardneri* is slow, taking about five months (George 1980). The seed capsule is unusual in that it lacks any ribs and does not dry out and split to release the seeds. Nor does the stem elongate to carry the capsules above the ground for wind dispersal. Instead the capsule develops into a smooth, cylindrical, succulent fruit, which remains moist and contains up to 50 seeds, about 0.7 mm long (large for an orchid). The method of seed dispersal is unknown, but it is possible the fruits are dug up and eaten by small marsupials such as bandicoots, the seeds passing through into the faeces (George 1980). Experiments on caged animals (Dixon 1982) showed that native rodents will consume seed pods and that seeds pass into the faeces undamaged, their thick coats resisting digestion.

George (1980) proposed that seed dispersal in *R. gardneri* parallels that of some ground fungi, which are eaten by woylies and other marsupials. He speculated that the strong formalin-like odour of cut flowers may repel marsupials from plants with immature seed capsules and predicted that the odour would disappear when the capsules mature. It may be that the capitulum of *R. gardneri* mimics the fruiting bodies of soil fungi, which may have similar texture, habit, and locations in the soil.

Attempts to locate potential seed-dispersing marsupials at known sites of *R. gardneri* have been unsuccessful (Dixon 1985). Many species of marsupials formerly common in the wheat belt of Western Australia are now extinct due to land clearing and predation by introduced cats and foxes, and it may be that *R. gardneri* survives today mainly by vegetative reproduction (Hoffman and Brown 1984).

Nothing is known of the pollination of *R. slateri* in eastern Australia. Rupp (1934) found fresh mature flower heads at depths of two centimetres or more below the soil surface, but old withered heads were generally found level with the surface below the leaf litter. From this Rupp (1934) surmised that after fertilization the stem must elongate slightly to bring the capsules to the surface. How seed dispersal is effected is unknown, but Rupp (1934) suggested that it may occur during rainstorms, perhaps by splashing (Dixon 1985) or by flowing water. The scarcity of the plant led Rupp (1934) to suggest that successful germination is rare. However, some evidence indicated *R. slateri* may reproduce vegetatively by breaking of rhizome branches to form clones of independent plants (Rupp 1934), as in *R. gardneri* (George 1980).

Rupp (1934) suggested the subterranean habit of *R. slateri* may indicate self-pollination but did not rule out the possibility that burrowing insects may be attracted to the flowers. However, observations by Rupp (1934) showed that the pollinia are well separated from the stigma by the rostellum and that no pollen was able to reach the stigma, although it may fall on the back of the rostellum in some cases. A pair of peculiar, slender column appendages, looking rather like tiny chains of beads on either side of the rostellum, may assist in holding the pollinia in place. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Not known in cultivation. **(HR)**

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SUBTRIBE THELYMITRINAE

Thelymitrinae Lindl., *Gen. Sp. Orch. Pl.*, 442 (1840) (as Thelymitridae). Type: *Thelymitra* J. Forst. & G. Forst.

Tribe Thelymitreae (Lindl.) Endl., *Mant. Bot. Suppl.*, **2**, 21 (1842).

Subfamily Thelymitroideae (Lindl.) Szlach., *Fragm. Flor. Geobot.*, **36 (1)**, 35 (1991).

Description

Glabrous or hirsute, tuberous geophytic *herbs. Tubers* elongate, naked. *Leaf* solitary, rarely absent, sessile, either cylindrical and terete or convolute, flat or channelled, sessile, erect, sometimes spirally twisted. *Inflorescence* racemose. *Flowers* resupinate, dull to brightly coloured; tepals subsimilar or dissimilar. *Labellum* fixed to the base of the column; lamina unlobed or obscurely lobed, either lacking calli or with a basal tuft of pseudoanthers or with hair-like trichomes; nectar absent. *Column* with a foot; pollinarium present; pollinia two or four. *Fruit* a dehiscent capsule. **(DJ)**

Anatomy

Leaf

SURFACE

Papillae present, one per cell, in various species. Epidermis: cells elliptical, rectangular to polygonal, often axially elongated; walls thick with conspicuous pit-fields. Stomata on both surfaces of dorsiventral leaves or all surfaces of terete leaves.

TRANSECTION

Dorsiventral or terete depending on species. Cuticle thin to moderately thick, smooth to striate depending on the species. Epidermis: cells isodiametric, elliptical, rectangular to papillate; outer wall thick; cells in *Thelymitra benthamiana* Lindl. rich in anthocyanins. Stomata superficial, substomatal chambers shallow. Mesophyll variable depending on species. If heterogeneous, 1–5 palisade layers on both surfaces of leaf (abaxial only in *Epiblema*). Extensive lacunae present in some species. Vascular bundles as for the tribe, in one ring in unifacial species immediately internal to palisade mesophyll, or in 1–2 rows with or without accessory vascular bundles in midrib below midvein. Crystals: raphides or rod-shaped crystals in mesophyll idioblasts of most species and in epidermis of *Calochilus herbaceus* Lindl.

Stem

TRANSECTION

Enclosed by bract, 2–5 cells wide in *Epiblema*; vascularized by three collateral strands. Hairs absent. Cuticle thin, smooth to striate. Epidermis: cells isodiametric, elliptical, rectangular, polygonal to S-shaped; outer wall thickened. Pelotons present in epidermal cells of *T. benthamiana*. Stomata absent or present and superficial, depending on the species. Cortex parenchymatous, innermost layers sclerotic, forming a sclerenchyma sheath in all species except *T. cyanea* (Lindl.) Benth. and *T. graminea* Lindl. Vascular bundles collateral, in 1–3 rings, the outer ring abutting sclerenchyma sheath. Xylem tracheids with annular, helical, scalariform or pitted thickenings. Crystals: raphides or rod-shaped crystals infrequent in cortex and/or pith.

Tuber

TRANSECTION

Hairs absent. Velamen 1–2 layered, cells elliptical, dome-shaped to polygonal, often periclinally compressed; walls of uniform thickness or differentially thickened, depending on species. Exodermis: cells elliptical to polygonal; walls of uniform thickness or differentially thickened, depending on species. Cortex parenchymatous, filled with starch grains in varying degrees. Outer layers dissociated in some species. Endodermis: cells elliptical, rectangular to polygonal. Stele medullated, polyarch (9–100, depending on species). Xylem tracheids with helical, scalariform or pitted thickenings. Crystals: raphides in outer cortex of many species.

Root

TRANSECTION

Hairs absent. Velamen 1–2 layered, cells elliptical to irregularly polygonal, often periclinally compressed; walls uniformly thickened or else outer wall and/or radial walls thicker, depending on species. Exodermis: cells elliptical to polygonal, walls uniformly thickened or outer and radial walls thicker, depending on species. Cortex parenchymatous, variously infected with hyphae and pelotons. Endodermis: cells elliptical to polygonal. Stele medullated, 3–9 arch. Xylem tracheids with annular, helical, scalariform, or pitted thickenings. Crystals: raphides and/or rod-shaped crystals in cortex. **(AP)**

Phytochemistry

Phytochemical data reported in the literature for Thelymitrinae are limited to *Thelymitra* (see entry above for *Elythranthera*). **(NV, RG)**

Phylogenetics

Thelymitrinae have always been linked to Diuridinae and Diurideae, although their status has been subject to change. When originally created by Lindley (1840), Thelymitrinae were treated at the same rank (a division) as Diurideae (= tribe) and was characterized by the labellum, petals, and sepals being similar in shape and petaloid. *Thelymitra* and *Epiblema* were included in the taxon. Endlicher (1842) followed Lindley's interpretation, but Bentham and Hooker (1883) treated these genera within a more broadly circumscribed Diurideae.

The relatively unusual situation of having the anther nestled within a mitra rather than as part of the column was interpreted by Szlachetko (1991) in the extreme, elevating the taxon to subfamily status. This treatment is inappropriate as shown by Clements (1995) with embryological studies; species of *Thelymitra*, *Calochilus*, and *Epiblema* all have a near-identical (diurid type) embryological developmental pattern. Furthermore, phylogenetic analyses of DNA sequences (Cameron *et al.* 1999; Kores *et al.* 1997, 2000; Clements *et al.*, in preparation), Theymitrinae are clearly part of the Diurideae within Orchidoideae.

Burns-Balogh and Funk (1986*a*, *b*) likewise had difficulty in interpreting the relationships of this subtribe, preferring instead to treat it within their subfamily Neottioideae rather than as part of Orchidoideae. They based this conclusion on the fact that staminodia are separated from the remainder of the column, which they considered primitive. Such an approach overlooks other well-established similarities between Thelymitrinae and members of Diurideae, such as the possession of root tubers, which historically have been used to link these taxa.

In a study using ITS sequences of nuclear ribosomal DNA, Clements *et al.* (in preparation) confirm the monophyly of *Thelymitra*, *Calochilus*, and *Epiblema* as well as grouping them together in a distinct clade. **(MAC)**

Artificial key to genera of Thelymitrinae (DJ)

1. • Sepals markedly dissimilar to the petals; most or all of the labellum ventral surface ornamented with papillae, calli, or trichomes .... **53. *Calochilus***
   • Sepals and petals subsimilar; labellum lacking papillae, calli or trichomes or with a basal tuft of linear calli 2
2. • Labellum lacking papillae, calli or trichomes; column much longer than wide; mitra fully fused and surrounding the column .... **55. *Thelymitra***
   • Labellum with a basal tuft of linear calli; column about as wide as long; mitra partially free and surrounding the column as broad wings .... **54. *Epiblema***

53. CALOCHILUS

Calochilus R.Br. *Prodr.*, 320 (1810). Type species: *Calochilus paludosus* R.Br.

Derivation of name

From the Greek *kalos*, beautiful, and *cheilos*, lip, referring to the remarkable labellum, which in most species is covered with lustrous, hair-like calli. **(DJ)**

Description (Plates 68, 69; Fig. 53.1)

Perennial geophytic *herbs*. *Roots* filamentous. *Tubers* ovoid to obovoid, paired, fleshy, naked; replacement tubers produced on the end of short droppers; daughter tubers absent. *Stem* erect, short, unbranched, terete, with membranous cataphylls at each node. *Leaf* single, basal, solitary, sessile, convolute in bud, rarely absent and replaced by sheathing bracts; lamina much longer than wide, fleshy, ribbed, often trigonous in section, canaliculate; venation anastomosing. *Inflorescence* racemose, 1–many flowered, erect, terminal; scape slender to stout, with 2–5 sterile bracts; floral bracts foliaceous, sheathing. *Flowers* resupinate, dull coloured, pedicellate; perianth often responding to hot weather by spreading widely. *Dorsal sepal* free, broader than the lateral sepals, concave, cucullate over the column. *Lateral sepals* free. *Petals* free, much smaller than the sepals, glandular, asymmetrically expanded on the upper margin, the apex often uncinate. *Labellum* free, attached by its base to the column base, markedly dissimilar in shape and size to the sepals and petals, ecalcarate; lamina obscurely lobed, margins entire or cut into narrowly linear, tapered, tooth-like lobes, either smooth or glandular, the apex often extended and ligulate to caudiform; dorsal surface usually glandular; callus consisting of elongate, colourful, hair-like calli, those toward the base reduced to tubercles, ridges, or plates, rarely the whole surface with tubercles or smooth; nectar absent. *Column* short, nearly as wide as long; column wings fused and partially surrounding the column to form a mitra; anterior base of mitra forming a rim or ridge in front of the stigma base; dorsal apex of the mitra vestigial; anterior margins of the mitra free, projecting forwards as obtuse wings, the interior basal surface in some species ornamented with one or more dark, shiny, eye-like spots, the dorsal surface of the wings with glandular excrescences; column foot absent; anther dorsal, non-rostrate, often emarginate, two-celled, persistent, basifixed; pollinarium consisting of four pollinia weakly attached to a viscidium; pollinia crescentic, pale yellow, mealy, friable; viscidium dorsal; rostellum apical; stigma entire, sunken. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, glabrous, erect; pedicels elongating slightly in fruit. *Seeds* numerous, light-coloured, winged. **(DJ)**

Distribution (Fig. 53.2)

A genus of about 23 species distributed in Australia, New Zealand, New Guinea, and New Caledonia. **(DJ)**

Palynology

Monads of *C. grandiflorus* (Benth.) Domin are mostly globose-oblate, *c.* 25 μm; monoaperturate, simple, porate; semitectate; reticulate with psilate to scabrate muri; heteropolar; and radiosymmetric (Ackerman and Williams 1981). **(AP)**

Ecology

Calochilus is distributed from about 8° south in Papua New Guinea to about 43° south in Tasmania, occupying a range of mesic habitats from the coast to montane zones. All species of *Calochilus* are terrestrials and reproduce solely from seed, growing as scattered individuals or in loose groups. Habitats in temperate Australia include slopes and ridges in sclerophyll forest and woodland; heathland, mallee shrubland over limestone, and hummocks in moist to wet swamps. In tropical Australia and New Guinea these orchids grow in moist to wet grassy areas in forests and grassland. In New Zealand they occur in a range of moist forests and shrublands, swamps, bogs and embankments. In New Caledonia *C. neocaledonicum* Schltr. grows in sparse maquis developed on rocky, ultrabasic soils.

They occur in seasonal climates and have periods of active growth and dormancy. In the tropics this is closely tied in with the wet season, the plants mostly completing their life cycle before the onset of the dry season. In temperate regions the plants grow in autumn and winter, flower in spring and early summer before dying back to dormant tubers during excessive heat and dryness. In temperate regions the leaves are fully developed prior to flowering,

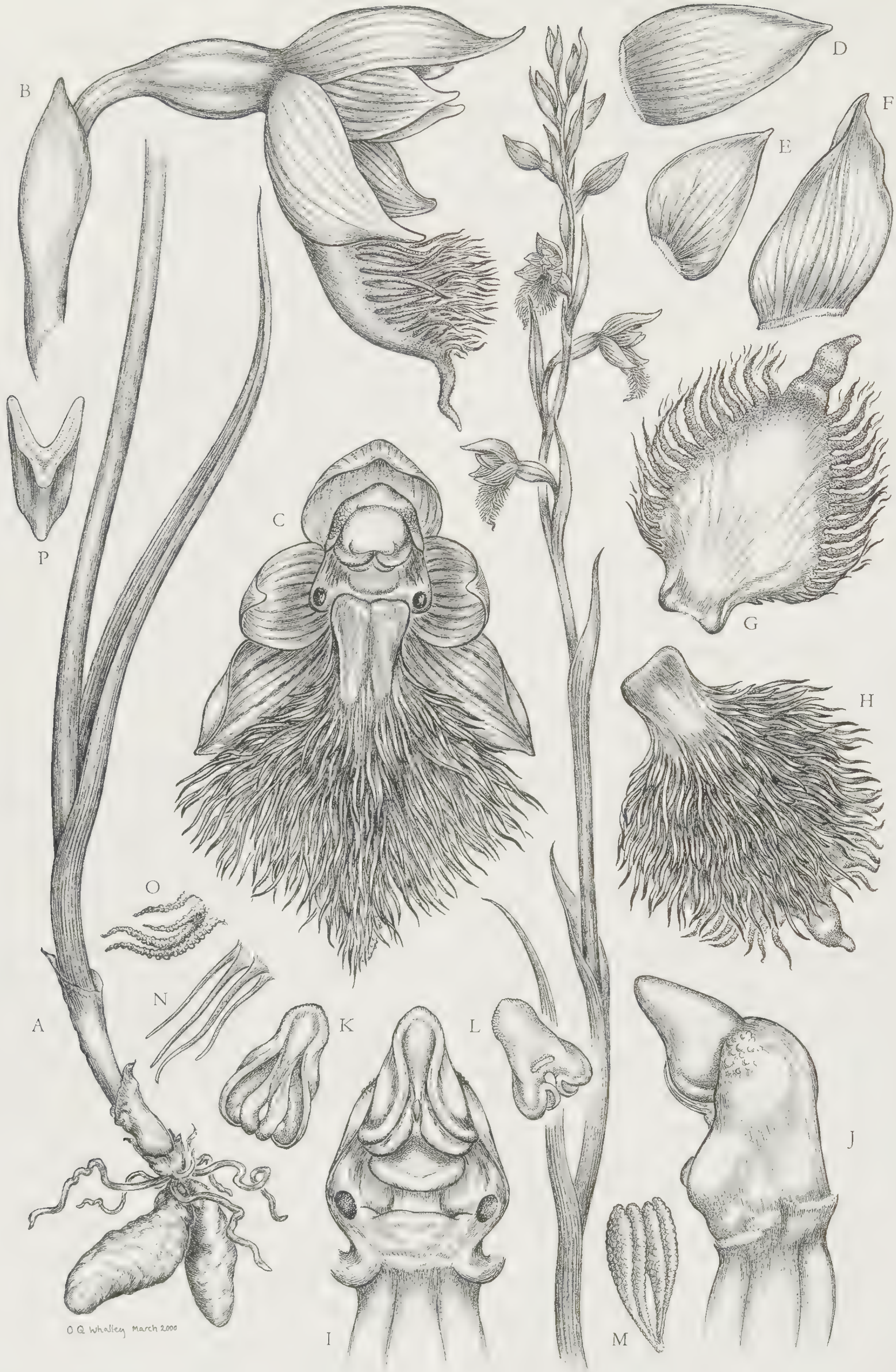

Fig. 53.1. *Calochilus campestris* R.Br. A. Habit, ×0.9; B. Flower from side, ×4.05; C. Flower from front, ×5.4; D. Dorsal sepal, ×4.05; E. Petal, ×4.05; F. Lateral sepal, ×4.05; G. Labellum from below, ×5.4; H. Labellum from above, ×5.4; I. Column from front, ×6.75; J. Column from side, ×6.75; K. Anther from front, ×5.4; L. Anther from behind, ×4.5; M. Pollinarium (after W. H. Nicholls, 1969), ×8.1; N. Labellum hairs, ×6.75; O. Labellum hairs from margin, ×6.75; P. Leaf transection, ×2.7. Drawn by Oliver Q. Whalley from Kew Spirit Collection nos. 55520 and 53222.

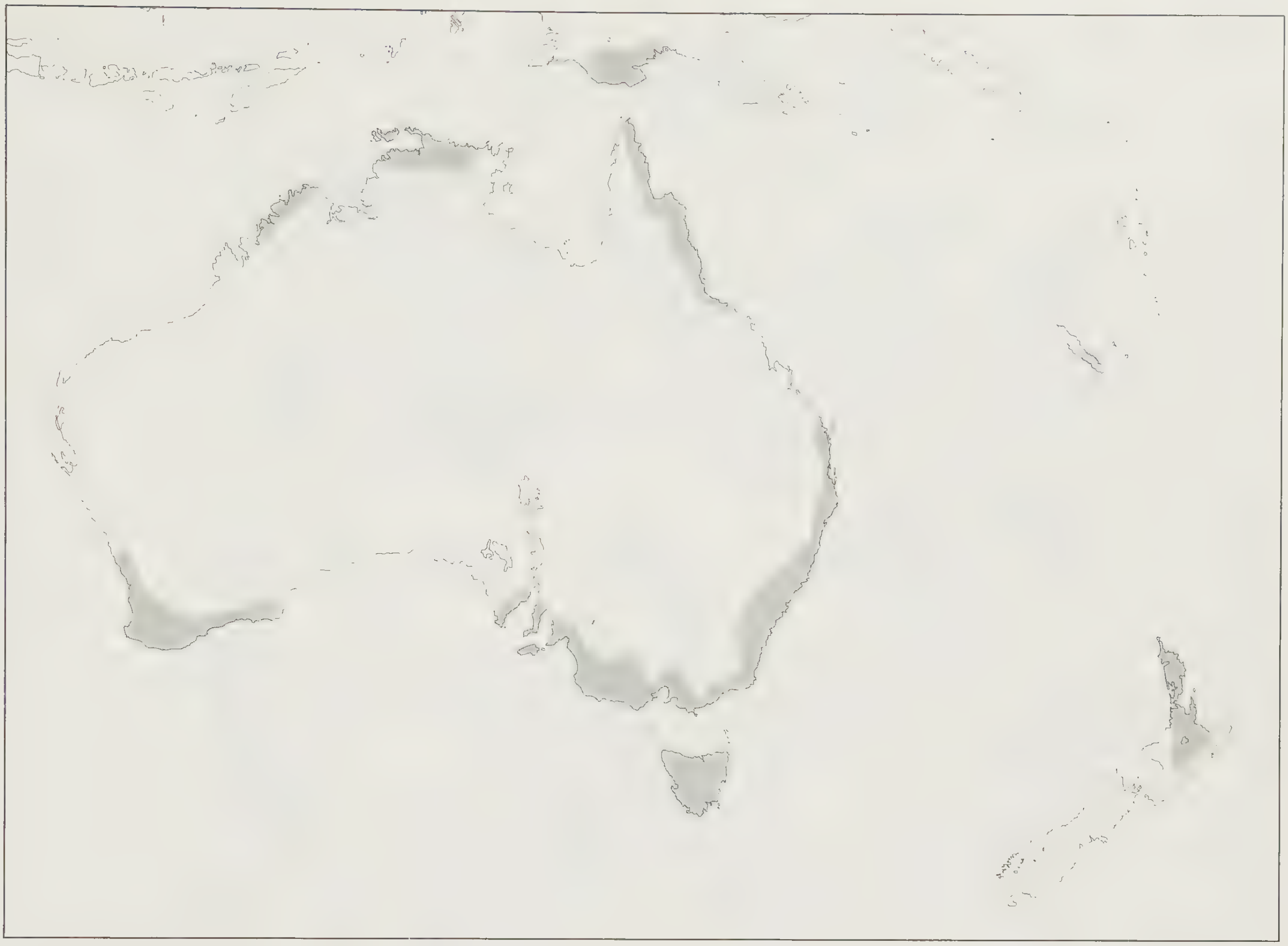

Fig. 53.2. Distribution map of *Calochilus*.

whereas in many of the tropical species the leaf is only partially developed at anthesis and continues growth after the seeds are shed. Seed dispersal begins 6–12 weeks after pollination.

The perianth of *Calochilus* expands freely without the influence of sun, but it is noticeable on hot sunny days that the perianth of some species expands even more widely than usual and often partly recurves. **(DJ)**

Pollination

There have been no systematic scientific studies of the pollination of any *Calochilus* species. Current knowledge is based on limited field observations and anatomical studies. In general it is considered that most, if not all, *Calochilus* species are autogamous (Cady 1972; Jones and Gray 1974; Bates 1978*c*; Jones 1988). However, at least some species also attract scoliid wasps, *Campsomeris*, by sexual deception (Fordham 1946; Jones and Gray 1974; Bower and Branwhite 1993), allowing some outcrossing to occur. Species that attract *Campsomeris* wasps are therefore facultatively autogamous, self-pollination occurring if pollinia are not removed by the vector (Jones and Gray 1974). *Calochilus* species provide no nectar (Jones and Gray 1974) and have no obvious odour (Fordham 1946; Jones and Gray 1974).

The column structure of *Calochilus* is adapted for a simple form of autogamy. In all species the anther projects forward above the stigma, allowing the pollinia to fall or crumble downward onto its upper edge. Cady (1972) provided details of obligate autogamy in *C. campestris* R.Br. in populations on the south coast of New South Wales in which all ovaries developed capsules. After anthesis, Cady found it was impossible for an external agent to remove the pollinia. In the late bud stage the rostellum became viscid and sent out root-like growths that adhered to the apices of the pollinia. However, just prior to this the anther cells split, and pollinia began to break up, crumbling onto the upper edge of the stigmatic surface where they germinated. By anthesis the pollinia were attached firmly to both the rostellum and stigma and could not be removed.

By contrast, Fordham (1946) reported that pollinia were readily removed from flowers of *C. campestris* by the wasp *Campsomeris tasmaniensis* on the north coast of New South Wales. Picked flowers were visited by four wasps carrying pollinaria on the front of the head, one with two sets. One was observed to pollinate a flower and also remove the pollinarium from the same flower. Wasps would circle the vase of flowers, hover in front of them, advance, and retreat a short distance several times before landing on the long hairs of the labellum. The wasps then curved their abdomens, probing the ribbon-like labellum apex with everted genitalia. Fordham interpreted these copulatory actions as 'stinging' movements, apparently assuming the wasp was a female attempting to subdue a prey insect on which it would later lay its eggs. This interpretation was taken up by van der Pijl and Dodson (1966), who erected a 'pseudoparasitism' pollination syndrome for it. The likely error was pointed out by Jones and Gray (1974) and Armstrong (1979). Bower and Branwhite (1993) showed that pseudoparasitism was not involved in *C. campestris* by noting the overlooked fact that Fordham's specimens had been identified as males.

As *Campsomeris tasmaniensis* males attempted to couple with the labellum they moved toward the short column and pushed their heads against it, thereby contacting the viscidium, and removing the pollinarium as they retreated (Fordham 1946). Similar behaviour by a single *C. tasmaniensis* on *C. campestris* was reported by Bower and Branwhite (1993). However, in this case removal of whole pollinaria was not observed. Rather, the wasp's vigorous actions on the labellum broke up the pollinia, leaving fragments on its face and possibly the stigma.

The limited observations on *C. campestris* indicate there are differences among populations in the relative degrees of insect-mediated outcrossing and autogamy. At the extremes are obligately autogamous populations (Cady 1972) in which the pollinia cannot be removed and outcrossing populations in which whole pollinaria are easily removed (Fordham 1946). In between may be populations in which partial pollinia are removed (Bower and Branwhite 1993).

The latter situation also occurs in *C. caeruleus* L. O. Williams (as *C. holtzei* F. Muell. in Jones and Gray 1974), which is pollinated by males of an undescribed species of *Campsomeris*. The behaviour of males on the flowers of *C. caeruleus* is similar to that of *Campsomeris tasmaniensis* on *C. campestris*. *Calochilus caeruleus* was highly attractive to wasps on warm sunny days with some 30 males being captured in a day using a single inflorescence as bait (Jones and Gray 1974). Struggles for possession ensued when several males arrived simultaneously. No other insects were attracted, and the scoliids made no attempt to feed. Wasps were able to locate hidden flowers, indicating the primary means of attraction was by odour, almost certainly a mimic of the female sex pheromone. The source of the odour in *Calochilus* species is unknown. Attracted wasps rapidly approached flowers low over the ground and circled them three or four times before landing on a labellum. Close range visual orientation appears to involve the reddish labellum hairs. Wasps were highly attracted to the red lettering on a camera near a hidden inflorescence. Once on the labellum wasps made copulatory movements with the abdomen, which pushed the head against the column. Visits lasted only 10–15 seconds after which they went to another flower on the raceme or circled it.

Rather than removing the whole pollinarium, the vigorous copulatory actions of male *Campsomeris* sp. visitors to *C. caeruleus* tended to break up the friable pollinia and pushed much of it onto the stigma. Some was removed on the wasp's forehead for potential cross-pollination of flowers on other plants. It seems clear that pollination by *Campsomeris* sp. in *C. caeruleus* results in autogamy, geitonogamy, and a small amount of potential outcrossing (Jones and Gray 1974).

The limited available observations suggest that each insect-pollinated species of *Calochilus* attracts only sexually deceived males of a single *Campsomeris* species. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Plants are difficult to maintain in cultivation for more than two or three years. **(HR)**

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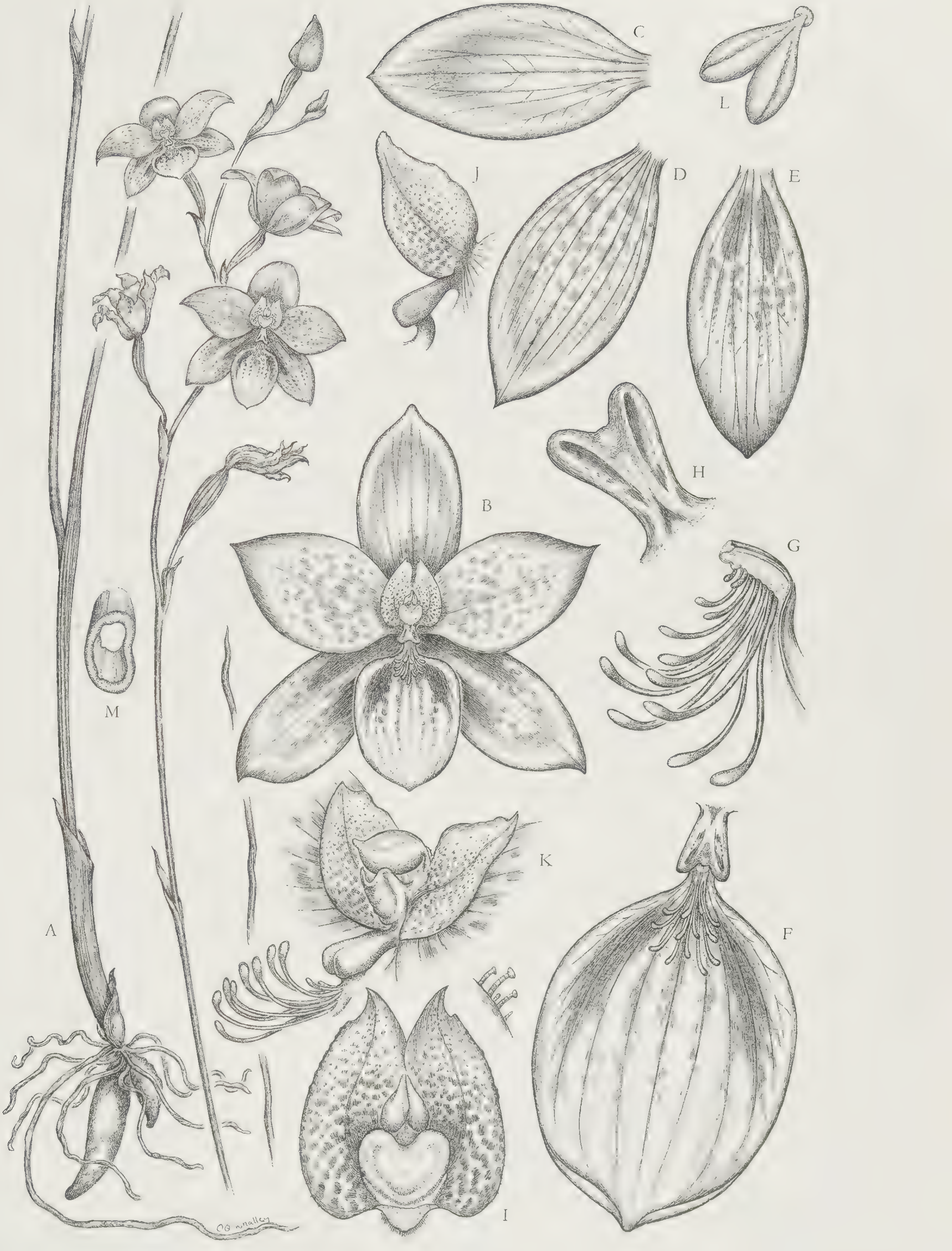

Fig. 54.1. *Epiblema grandiflorum* R.Br. A. Habit, ×1; B. Flower from front, ×3; C. Dorsal sepal, ×3; D. Petal, ×3; E. Lateral sepal, ×3; F. Labellum from above, ×4.5; G. Labellum calli, ×9; H. Basal gland of labellum from above, ×9; I. Column from front, ×9; J. Column and basal gland of labellum from side, ×4.5; K. Anther and stigma (column wing folded back), ×4.5; L. Pollinarium, ×9; M. Leaf, transverse section, ×18. Drawn by Oliver Q. Whalley from Kew Spirit Collection nos. 9108 and 40500.

54. EPIBLEMA

Epiblema R.Br., *Prodr.*, 315 (1810). Type species: *Epiblema grandiflorum* R.Br.

Derivation of name

From the Greek *epi-*, upon, over, and *blema*, cowl, coverlet, probably referring to the the large mitra that covers the column. **(DJ)**

Description (Plate 70; Fig. 54.1)

Perennial geophytic *herbs*. *Roots* filamentous. *Tubers* ovoid, paired, fleshy, naked; replacement tubers formed on the end of short droppers; daughter tubers formed on the end of short root-like stolons. *Stem* erect, short, unbranched, terete, with membranous or fibrous cataphylls at each node. *Leaf* single, basal, convolute, sessile; lamina much longer than wide, erect, terete, hollow, glabrous. *Inflorescence* racemose, 1–many flowered, erect, terminal; scape wiry, with one or two sterile bracts; floral bracts closely sheathing. *Flowers* resupinate, brightly coloured, pedicellate. *Sepals* free, subsimilar, somewhat dissimilar to the petals. *Petals* free. *Labellum* free, attached by a short claw to the anterior column base, dissimilar in shape to the sepals and petals, ecalcarate; lamina not lobed, the margins entire, apex broadly obtuse to apiculate; callus consisting of a basal swelling, entire or bilobed, with a terminal tuft of projecting, pseudoantherous, filiform-clavate appendages; nectar absent. *Column* with wings, the free parts surrounding the column to form a broad mitra, the lateral arms erect and extending much higher than the anther, the anterior margins slightly irregular and bearing short glandular trichomes; column foot absent; anther basifixed, erect and parallel to the axis of the column, rostrate; pollinarium consisting of two pollinia attached directly to a viscidium; pollinia white, soft, mealy; viscidium terminal; stigma entire, cordate; rostellum apical. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, erect, glabrous; pedicels not elongating in fruit. *Seeds* numerous, light coloured, winged. **(DJ)**

Distribution (Fig. 54.2)

A monospecific genus endemic in south-western Western Australia. **(DJ)**

Palynology

Monads of *E. grandiflorum* are globose-spherical, about 19 μm; monoaperturate, simple tenuate-porate; semitectate; reticulate; heteropolar; and radiosymmetric (Ackerman and Williams 1981). **(AP)**

Ecology

Epiblema grandiflorum is distributed in a narrow coastal band between about 31°south and 35°10′ south. The plants occur in tufts and colonies, reproducing from seed and forming clonal colonies by the production of daughter tubers on the end of root-like stolons. Plants grow in winter and spring, and the leaf is fully developed

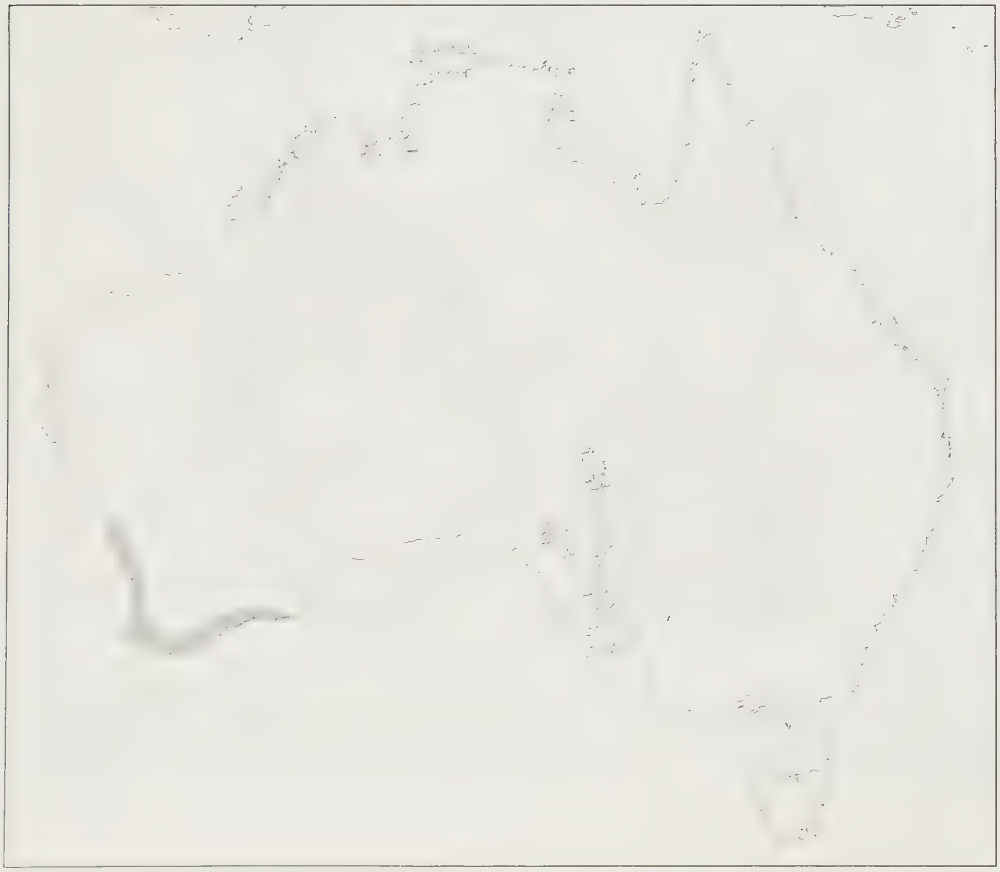

Fig. 54.2. Distribution map of *Epiblema.*

prior to flowering. The developing inflorescence grows up the centre of the hollow leaf and breaks through prior to flowering, which occurs in late spring and summer. Seed dispersal begins 8–12 weeks after pollination. This orchid grows in coastal and near-coastal peaty swamps that are inundated during winter and dry out during late spring and summer. **(DJ)**

Pollination

No studies of pollination of *Epiblema* (Burns-Balogh and Bernhardt 1988) have been reported, except that Jones (1988) indicated that it is not self-pollinating. The purple or blue perianth colours and radial symmetry are consistent with flowers advertising rewards of nectar and pollen to bees, wasps, and flies. Radial spotting on the perianth and the broad purple lines on the labellum and lateral sepals probably guide pollinators to the centre of the flower. The flowers are nectarless, indicating that *E. grandiflora* is a food mimic (Burns-Balogh and Bernhardt 1988).

The labellum has a prominent basal appendage with two pale, rounded lobes from the anterior, from which arises a set of forward-projecting, stamen-like filaments (Cady and Rotherham 1970) with pale clubbed heads. This structure is a putative pseudoanther. The most likely mode of pollination in *Epiblema* is that pollen- and nectar-seeking bees attempt to gather pollen from the pseudoanther with their legs while their heads, possibly probing for nectar at the labellum base, press against the column. The viscidium in the upper margin of the stigma would attach to the face of the bees in the same manner as in *Diuris*.

Burns-Balogh and Bernhardt (1988) suggested that *Epiblema* is a mimic of co-blooming papilionoid legumes. The bilobed basal appendage somewhat resembles the grooved labellum callus of many *Diuris* species, which appears to mimic the gap between the wing petals of papilionoids. The mimicry is further enhanced by the shape of the pseudoanther filaments, which are strongly papilionaceous and lacking in *Diuris*. Whether *Epiblema* mimics a specific co-flowering papilionoid genus or is a more generalized mimic remains to be determined. **(CCB)**

Uses

None recorded. **(DJ)**

Cultivation

Not known in cultivation. **(HR)**

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55. THELYMITRA

Thelymitra J. Forst. & G. Forst., *Char. Gen. Pl.*, **97**, t. 49 (1776).
Type species: *Thelymitra longifolia* J. Forst. & G. Forst.
Macdonaldia Lindl., *Edward's Bot. Reg.*, 1–23, *Swan. Riv. Append.* l (1840). Type species: *Macdonaldia smithiana* Gunn ex Lindl.

Derivation of name

From the Greek *thelys*, female, and *mitra*, cap, turban or hat, referring to the mitra that subtends or covers the column of these orchids. **(DJ)**

Description (Plates 71–74; Fig. 55.1)

Perennial geophytic *herbs*. *Roots* filamentous. *Tubers* ovoid, paired, fleshy, naked; replacement tubers formed on the end of short droppers, sometimes extra daughter tubers formed in the same manner, rarely daughter tubers formed on the end of root-like stolons. *Stem* erect, short, unbranched, terete, with membranous cataphylls at each node. *Leaf* single, basal, convolute, sessile; lamina usually much longer than wide, usually erect, terete, canaliculate or flat, sometimes twisted spirally, glabrous or hairy, often ribbed dorsally. *Inflorescence* racemose, 1–many flowered, erect, terminal; scape wiry, sometimes flexuose, with 1–3 sterile bracts; floral bracts foliaceous, sheathing. *Flowers* resupinate, brightly coloured, shortly pedicellate, the perianth usually spreading in response to sunshine, opening freely or tardily or cleistogamous. *Sepals* free, usually all similar or the dorsal sepal broader. *Petals* free, similar or dissimilar to the sepals. *Labellum* free, attached by its base to the anterior column base, usually similar in shape and size to the sepals and petals, sometimes broader or narrower, ecalcarate; lamina not lobed, unadorned, the margins entire or undulate; callus absent; nectar absent. *Column* with fused wings surrounding the column to form a mitra; anterior base of mitra forming an unadorned rim or ridge in front of the stigma, dorsal apex of mitra complex, usually tripartite with a central post-anther lobe and two lateral arms, sometimes extra auxiliary lobes or lobules flanking the post-anther lobe on the anterior side; post-anther lobe prominent or reduced, in one group elongate, tubular and cucullate, variously cleft, lobed or toothed apically, often differently coloured from the rest of the column, in another group much reduced and dorsally adorned with digitate calli; lateral arms with or without tufts of moniliform cilia; column foot absent; anther basifixed, erect and parallel to the axis of the column or porrect, rostrate or not; pollinarium consisting of two pollinia attached directly to a viscidium; pollinia white, soft, mealy; pollen grains in monads or tetrads; viscidium terminal or dorsal; stigma entire, quadrate, supported on a basal stalk; rostellum apical. *Ovary* elongate, ribbed, glabrous. *Capsules* dehiscent, glabrous, erect; pedicels not elongating in fruit. *Seeds* numerous, light-or dark-coloured, winged. **(DJ)**

Distribution (Fig. 55.2)

A genus of about 50 species distributed in Australia, New Zealand (including Stewart Island, Chatham Island, and Auckland Island), New Caledonia, New Guinea, Indonesia, and the Philippines. **(DJ)**

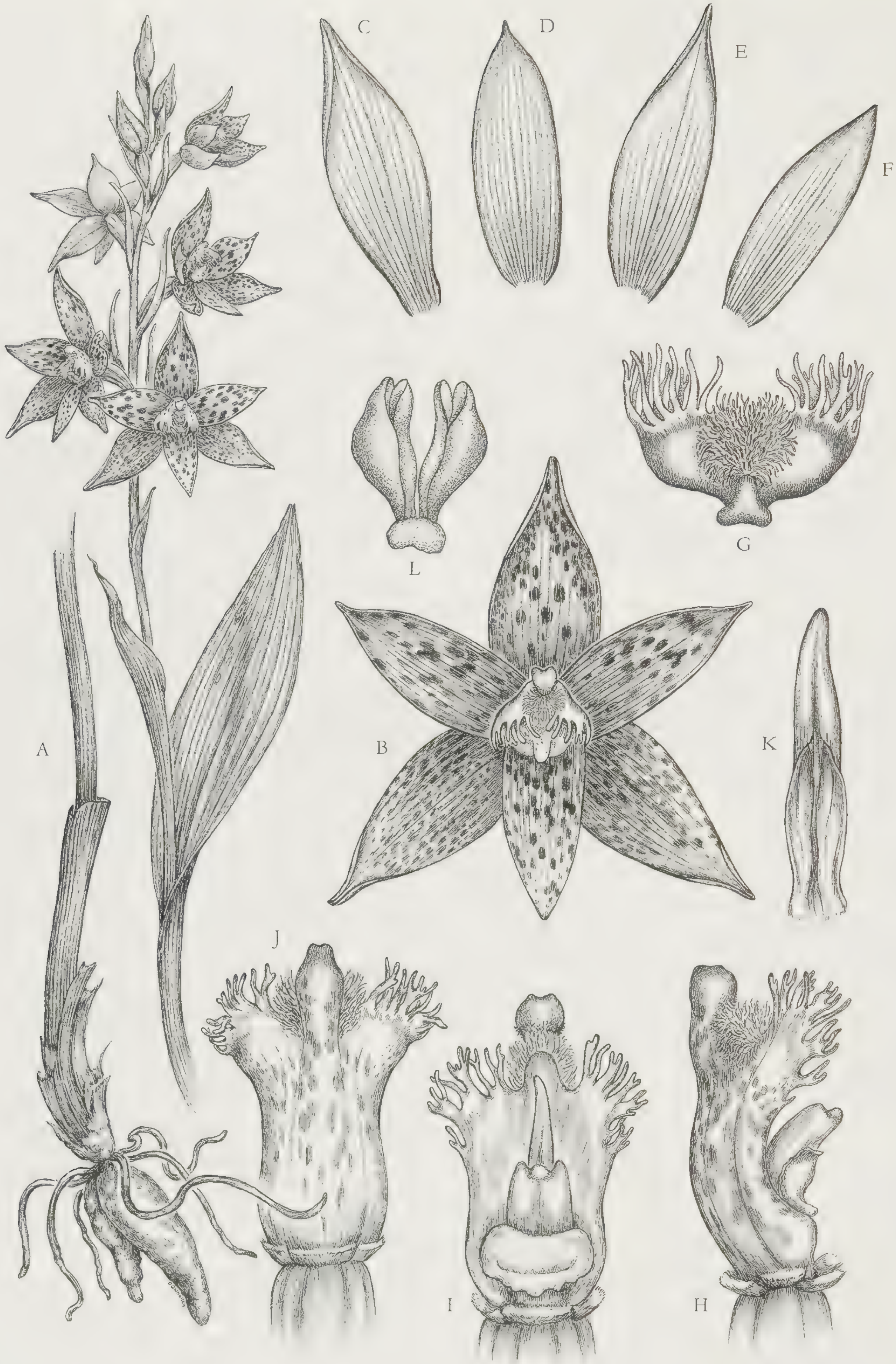

Fig. 55.1. *Thelymitra fuscolutea* R.Br. A. Habit, ×0.9; B. Flower from front, ×0.9; C. Dorsal sepal, ×2.7; D. Petal, ×2.7; E. Lateral sepal, ×2.7; F. Labellum, ×2.7; G. Column from above, ×8.1; H. Column from side, ×8.1; I. Column from front, ×8.1; J. Column from back, ×8.1; K. Anther cap, ×8.1; L. Pollinarium, ×8.1. Drawn by Oliver Q. Whalley from sheet from herbarium of Dr. A. Morrison (K).

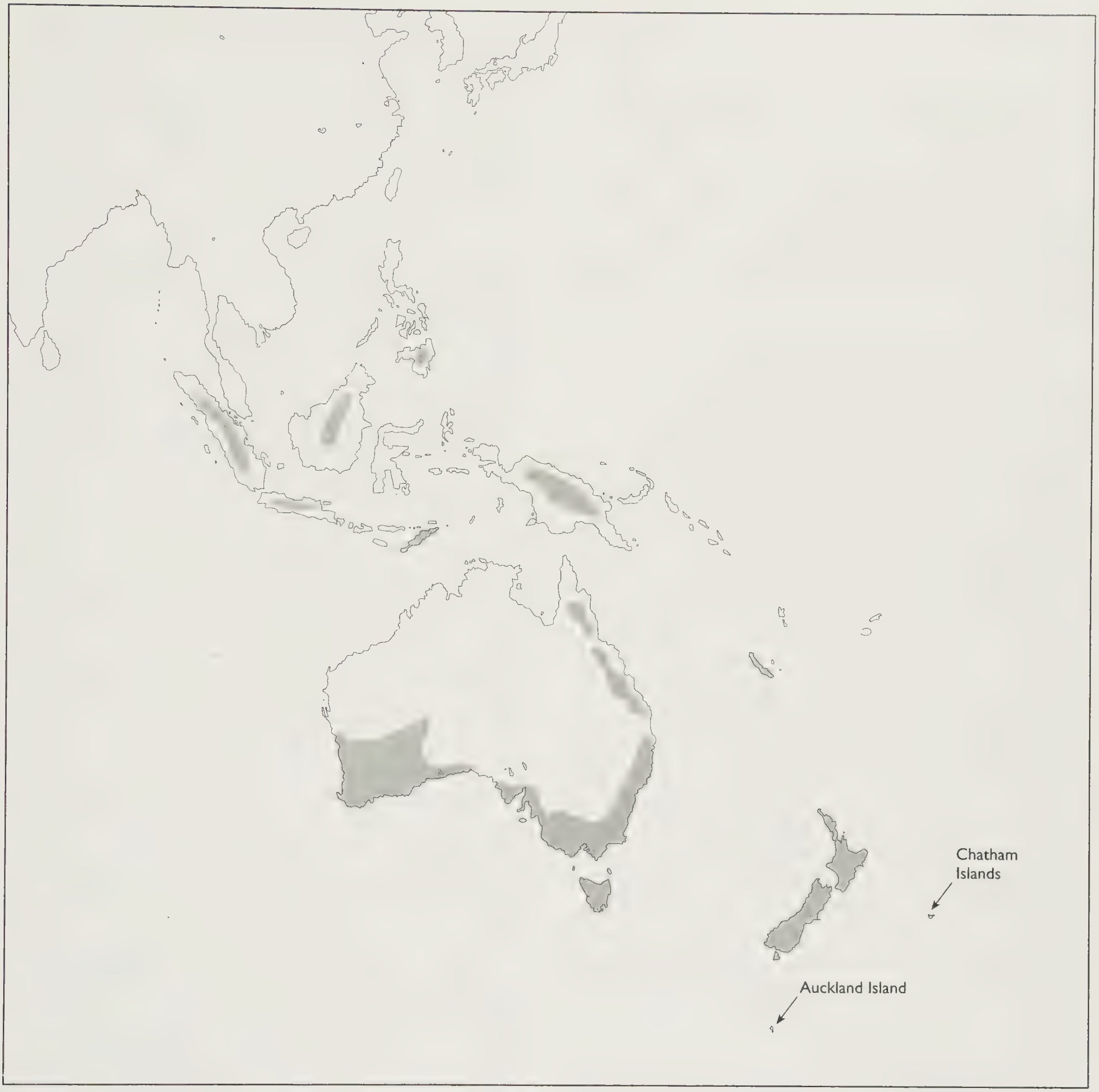

Fig. 55.2. Distribution map of *Thelymitra.*

Infrageneric treatment

The following sections have been described within *Thelymitra* but are not comprehensive and have limited application until a full revision of the genus can be undertaken. **(DJ)**

Thelymitra section **Cucullaria** Benth., *Fl. Aust.*, **6**, 317 (1873). Type species: *Thelymitra javanica* Blume.

Thelymitra section **Macdonaldia** Benth., *Fl. Aust.*, **6**, 317 (1873). Type species: *Thelymitra smithiana* (Gunn ex Lindl.) Benth.

Thelymitra section **Biaurella** Benth., *Fl. Aust.*, **6**, 317 (1873). Type species: *Thelymitra variegata* (Lindl.) F. Muell.

Thelymitra section **Thelymitra**.

Palynology

Tetrads of *T. ixioides* Sw. are *c.* 36 μm, tetrahedral; inaperturate; semitectate; reticulate; the units globose-spherical (Ackerman and Williams 1981). **(AP)**

Ecology

Although *Thelymitra* has its greatest diversity in Australia and New Zealand, it is much more widespread and has elements distributed from subantarctic islands to the tropics. Latitudinally *Thelymitra* is distributed from about 15° north in the Philippines to about 50°

south on Auckland Island. All species are terrestrial, most growing as individuals or in loose groups and reproducing solely from seed. A few species produce extra, replacement tubers to form localized tufts (*T. gregaria* D. L. Jones & M. A. Clem.) or develop daughter tubers on the end of root-like stolons to form colonies, as in *T. antennifera* (Lindl.) Hook.f. and *T. cyanea* (Lindl.) Benth. All species occur in seasonal climates and have periods of active growth and dormancy, the latter coinciding with times of low humidity, heat, and dryness. The leaves of all species are fully expanded prior to flowering. Seed dispersal begins 8–12 weeks after pollination.

Thelymitra species occur in a wide range of mesic habitats from the coast to montane and alpine zones. Habitats in Australia include slopes and ridges in sclerophyll forest and woodland; coastal scrub on consolidated dunes; heathland and sandplain vegetation; mallee shrubland over limestone; clefts and crevices in sandstone outcrops; sphagnum hummocks in moist to wet swamps, particularly in subalpine regions; and subalpine meadows. In New Zealand these orchids occur in a range of moist forests and shrublands, swamps, bogs, embankments, and alpine herbfields. In New Caledonia *T. sarasiniana* Kränzl. grows in maquis developed on ultrabasic soils. In New Guinea, Indonesia, and the Philippines species of *Thelymitra* mainly occur on mountains in forests, stunted scrub or among grass.

The perianth of most species of *Thelymitra* expands on hot sunny days, closing again at night. This behaviour has resulted in the apt vernacular of 'sun orchids' for the genus. The higher the diurnal temperature, the more rapidly and wider the flowers open. On days of high humidity the perianth expands even more readily and at lower temperatures than on drier days. Response to temperature varies with the taxon, and whereas flowers of some species may expand readily even on relatively cool days, others never open fully even in hot weather. Many species on mountain tops and in colder climates expand tardily, if at all, and cleistogamy is common in such areas. Flowering of *Thelymitra* occurs mainly over spring and summer, although *T. hiemalis* D. L. Jones & M. A. Clem. and *T. apiculata* (A. S. George) M. A. Clem. & D. L. Jones are unusual in their winter habit.

Hybridization appears to be relatively frequent in *Thelymitra* (McCrae and Molloy 1998), and there is evidence of speciation occurring via this process (Molloy and Dawson 1998; Peakall and Molloy 1998). **(DJ)**

Pollination

A number of recent scientific studies have been published on the pollination of *Thelymitra*, making it one of the better-understood Diurideae (Bernhardt and Burns-Balogh 1986*a*; Dafni and Calder 1987; Cropper and Calder 1990; Sydes and Calder 1993; Molloy and Dawson 1998). In addition, useful anatomical studies into column structure, from which aspects of pollination could be inferred, were performed by early workers (Fitzgerald 1875–93; Cheeseman 1881; Rogers 1913). These studies indicated that *Thelymitra* species exhibit a range of pollination mechanisms from obligate self-pollination verging on cleistogamy, through facultative self-pollination to obligate insect-mediated pollination.

Thelymitra is unusual among Orchidaceae in having unorchid-like brightly coloured, radially symmetrical, saucer-shaped flowers (Dressler 1981; Jones 1981; Burns-Balogh and Bernhardt 1988; Jones 1998*g*). Actinomorphy is due to the largely undifferentiated labellum that is almost identical to the other ovate-lanceolate petals in most species. The lack of differentiation in the corolla and the short column led some workers to regard *Thelymitra* as primitive (van der Pijl and Dodson 1966; Rasmussen 1982). By contrast Jones (1981) and Bernhardt and Burns-Balogh (1986*a*) considered that the column in *Thelymitra* had taken over the role of the labellum in attracting and manipulating pollinators, and Jones (1981) interpreted this as an advanced step in orchid evolution. Similarly, Burns-Balogh and Bernhardt (1988) concluded that the actinomorphic corollas of *Thelymitra* were derived from zygomorphic ancestors, but that this change was accompanied by the development of an increasingly ornate column.

Also unusual among orchids is the large number of *Thelymitra* species with blue flowers (Burns-Balogh and Bernhardt 1988). Over 50% of the 43 species listed in Jones (1988) are predominantly blue. Other flower colours include yellow, pink, purple, and brown. The corolla in some species is marked with darker spots or striations. *Thelymitra variegata* is highly variegated in shades of red, purple, and yellow (Jones 1988), and *T. epipactoides* F. Muell. has flowers with subtle shades of shining bronze, grey, greenish, and pink, often varying among plants (Cropper and Calder 1990).

A further distinctive feature of *Thelymitra* is the diurnal opening and closure of flowers in most species (Cady and Rotherham 1970; Jones 1988; Jones 1998*g*). An exception is *T. venosa* R.Br., flowers of which remain open throughout anthesis, even at night (Cady and Rotherham 1970; Jones 1988). Flowers of all other species close at night and reopen during the day in response to weather conditions. The precise conditions under which flowers open and close varies greatly between species and is correlated with the pollination mechanism (Bates and Weber 1990; Backhouse and Jeanes 1995; Jones 1998*g*). In general, self-pollinating species open only on hot days and then only for a relatively short time. By contrast, insect-pollinated species tend to open at lower temperatures and for longer periods. Flowers may open partially if the temperature does not become quite hot enough (Jones 1988; Jones 1998*g*).

The short column of *Thelymitra* features a prominent species-specific mitra or hood around the anther and stigma. The hood typically has three lobes: the post-anther lobe, which overtops the stigma and anther, and the lateral lobes, often referred to as arms or appendages, which usually project forward in front of the post-anther lobe from the upper lateral margins of the hood. There may also be a pair of mid-lobes between the lateral lobes and the post-anther lobe. The top of the post-anther lobe, the mid-lobes, and the free parts of the lateral lobes are usually highly ornamented in species-specific patterns. The post-anther lobe may be bright yellow or orange apically above a darker coloured band and may be smooth and rounded or covered in rugose papillae. The lateral lobes usually have contrasting colours and shapes. In many species in the *T. ixioides* and *T. longifolia* complexes the lateral lobes have terete arms terminated by white or pink brush-like trichome tufts. In the *T. venosa* complex the yellow lateral lobes are flattened and twisted. Many species have orange, yellow, or maroon, broad-rounded or club-like lateral lobes covered in papillae, e.g. *T. antennifera* and *T. carnea* R.Br., *Thelymitra fuscolutea* R.Br., and relatives have broad, flattened lateral lobes with fimbriate margins.

The position of the anther relative to the stigma also varies in *Thelymitra* (Fitzgerald 1875–93; Rogers 1913; Burns-Balogh and Bernhardt 1988) and greatly influences the pollination mechanism. Fitzgerald and Rogers observed that the anther may remain behind the stigma throughout floral development or that the column may lengthen carrying the anther above it. In columns in which the anther is carried upward the pollinia may be left behind if they first become attached to the rostellum, in which case they hang behind the stigma.

Fitzgerald considered the pollination mechanisms of 12 *Thelymitra* species in detail, and Rogers provided accounts of an additional five. However, neither observed flower visits by insects. Fitzgerald concluded that six species were obligately self-pollinating, four required the intervention of insects, and two would self-pollinate if insects did not remove the pollinia. Rogers found two adapted for insect pollination and three for autogamy.

Autogamy occurs in a variety of ways depending on the relative positions of the anther and pollinia. In *T. carnea*, *T. pauciflora* R.Br., *T. 'longifolia'* (probably actually a form of *T. pauciflora*) (Fitzgerald 1875–93), *T. luteocilium* Fitzg., and *T. cyanea* (Lindl.) Benth. (as *T. venosa*; Rogers 1913) the pollinia do not attach to the rostellum but are are carried upward with the anther and then crumble down upon the upper parts of the stigma. In *T. cyanea* the anther also tilts forward to project horizontally above the bowl formed by the angled stigma and the column wings, thereby distributing the pollen over the entire stigmatic surface. Autogamy occurs in the bud in *T. carnea*, *T. luteocilium*, and *T. cyanea*, confirmed in *T. carnea* by Molloy and Dawson (1998).

Thelymitra species in which the anther and pollinia remain behind the stigma self-pollinate either when the pollinia swell and spill over the edges of the stigma (*T. malvina* M. A. Clem., D. L. Jones & Molloy, cited as *T. nuda* R.Br.) or the edges of the stigma curl backward and contact the pollinia (*T. media*), or a combination of the two (*T. circumsepta* Fitzg.) according to Fitzgerald (1875–93). Sydes and Calder (1993) found that the pollinarium of Victorian populations of *T. circumsepta* could not be removed as a unit, that the stigma is thin and translucent with narrowed upper parts so that the pollinia can be seen behind and through it, and that the edges of the stigma contact the pollinia. Self-pollination in *T. fuscolutea* began when the apices of the pollinia collapsed forward onto the stigma. Further access of pollen to the stigma resulted from shrinkage of the rostellum and slight upward and forward movement of the anther (Rogers 1913).

Populations of *T. circumsepta* in the Blue Mountains west of Sydney often have columns with a 'frontal appendage', similar in its most developed forms to the lateral lobes of the hood (Fitzgerald 1875–93; Blackmore 1966). This lobe rises in front of the stigma and may have a terminal penicillate brush completely blocking access by pollinators to the stigma. However, the lobes vary greatly in height and are reduced in many flowers in the same populations to a vestigial knob (Blackmore 1966). Plants with fully developed frontal lobes also occur on the northern tablelands of New South Wales (Blackmore 1966) but are rare in Victoria where they are regarded as mutants (Backhouse and Jeanes 1995). Similar appendages have been recorded rarely in *T. fuscolutea*, and vestigial knobs sometimes occur in several other species (Blackmore 1966). Such abnormal appendages are of no consequence to obligately autogamous species.

Fitzgerald (1875–93) identified several common characteristics in autogamous *Thelymitra* species. They often have small flowers (except *T. circumsepta* and *T. media*) with friable pollinia (except *T. media*), and ovaries uniformly developing seed. He noted that whereas many self-pollinated species lack a connection between the pollinia and the rostellum, some species with such connections may be primarily self-pollinating, e.g. *T. media*. Sydes and Calder (1993) noted that only one flower of *T. circumsepta* opens at a time in contrast to most outcrossing species.

The flowers of most autogamous species tend to open only on hot days, e.g. *T. carnea* and *T. luteocilium* (Rogers 1913). *Thelymitra 'longifolia'* opens only for an hour or two in the middle of the day, and *T. pauciflora* only on hot sunny days (Fitzgerald 1875–93). *Thelymitra circumsepta* rarely opens fully and then requires high temperatures, 25–32°C and relative humidities of between 21%–66% (Sydes and Calder 1993). *Thelymitra cyanea*, on the other hand, opens freely on sunny days in the manner of insect-pollinated species (Rogers 1913; Jones 1971).

By contrast to the above some of the *Thelymitra* species identified as autogamous by Fitzgerald (1875–93), some such as *T. malvina* and *T. media*, produce impressive displays of many large flowers opening simultaneously. These species are likely to be facultatively autogamous. Jones (1981) observed native bees visiting and removing pollinaria from *T. media*, and Molloy (1990) regards *T. malvina* as outcrossing in New Zealand.

The existence of facultative autogamy in *Thelymitra* was clearly demonstrated by Cheeseman (1881) for *T. longifolia* in New Zealand. During bud development the anther of *T. longifolia* is behind the stigma and fully matures before the column lengthens. Well before anthesis the anther cells split, allowing the pollinia to become attached to the viscidium near their apices. The anther is then carried above the pollinarium on the lengthening column. *Thelymitra longifolia* opens freely on sunny days between about 09:00 and 17:00. In newly expanded flowers the pollinarium is easily withdrawn, but shortly after anthesis it can no longer be removed with the advent of self-pollination. Autogamy occurs when the margins of the membranous upper part of the stigma roll back to contact the pollinia hanging behind. Rapid penetration of the stigma by the pollen tubes bind the pollinarium so that by the second day of flowering it cannot be removed. In addition the apices of the pollinia collapse onto the stigma, and some pollen tubes grow through the thin stigma.

Cheeseman found that the rate of insect pollination is low in *T. longifolia*. He observed patches of flowers over a period of seven years and saw insects visit them only twice; on neither occasion were the pollinaria removed. Examination of flowers over three seasons in the field showed that only seven out of 223 (3.1%) had pollinaria removed. On only three occasions was pollen found scattered on the stigma. He concluded that *T. longifolia* was severely pollinator-limited and evolving toward self-fertilization.

Obligate or facultative autogamy is thought to predominate in 16 out of 19 (84%) New Zealand (Molloy 1990) and 50% of Australian (Jones 1988) *Thelymitra* species. Molloy concluded that the high proportion of autogamous species in the New Zealand flora (60%) is attributable to the low diversity of insects there, especially bees and wasps. However, given the high proportion of autogamous *Thelymitra* species in Australia, which has a relatively rich insect fauna, it would seem that *Thelymitra* is prone to the development of self-pollination.

The species considered to be insect-dependent by Fitzgerald (1875–93) had pollinia that attached to the viscidium and remained coherent, not swelling or crumbling. In these species many ovaries may not set seed in the field. Species identified as entomogamous by Fitzgerald were *T. megcalyptra* Fitzg., *T. rubra* Fitzg., *T. crinita* Lindl., and *T. fasciculata* Fitzg., but Rogers (1913) regarded *T. antennifera* and *T. macmillani* F. Muell. as insect-pollinated on similar grounds. Fitzgerald believed that *T. malvina* and *T. mucida* Fitzg. could be pollinated by insects because the pollinia are attached to the viscidium and can be withdrawn from an open flower. However, the pollinia are also quite friable, indicating that self-pollination could occur if the pollinarium is not removed.

All species of *Thelymitra* appear to lack nectar and edible pollen (Bernhardt and Burns-Balogh 1986*a*; Dafni and Calder 1987; Cropper and Calder 1990; Sydes and Calder 1993), although Bernhardt and Burns-Balogh observed syrphid flies apparently attempting to imbibe the mucilage on the stigma of *T. megcalyptra*. The attraction of pollinators most likely involves deception, and several modes have been suggested. Jones (1981) observed unidentified 'large fast flying bees' attempting to copulate (pseudocopulation) with the column of *T. media* R.Br. and *T. aristata* Lindl., implying that the complex hood ornamentation is an insect mimic. The bees landed on the column with their heads between the lateral lobes and made thrusting movements toward the stigma with the curled abdomen. Bates (1983*b*) reported that bees grappling with the column may have been attempting to fight off (pseudoaggression) an invader in their territory.

However, more recent studies (Bernhardt and Burns-Balogh 1986*a*; Dafni and Calder 1987; Burns-Balogh and Bernhardt 1988; Cropper and Calder 1990; Dafni and Bernhardt 1990; Sydes and Calder 1993) indicated that the hood is a complex pseudoanther, and visiting bees attempt to collect pollen from it. The hood structures mimic a variety of pollen sources, with single flowers often mimicking two kinds of anthers. Smooth post-anther lobes imitate poricidal anthers as do the ear-like lateral lobes of species such as *T. antennifera*. Papillate post-anther lobes may imitate clusters of short stamens as do the trichome brushes of the lateral lobes of many species. The grappling behaviour of bees on the hood is now thought to represent attempted 'buzzing' of poricidal anthers (*sensu* Buchman 1983) and scraping of pseudostamens for pollen by the legs (Plate 74). The probing actions seen by Jones (1981) were probably balancing movements by the abdomen as the bees clung to the narrow column crest.

Despite many hours of observation few insects have been seen visiting *Thelymitra* flowers (Bernhardt and Burns-Balogh 1986*a*; Dafni and Calder 1987; Cropper and Calder 1990; Sydes and Calder 1993). This is almost certainly because of deception mechanisms whereby bees learn to avoid unrewarding flowers. Outcrossing *Thelymitra* species attract vectors with visual and olfactory cues. They generally have spectacular visual displays of numerous large flowers opening simultaneously. Examples are *T. megcalyptra* (as *T. nuda*) (Bernhardt and Burns-Balogh 1986*a*), *T. ixioides* (Sydes and Calder 1993), and *T. epipactoides* (Cropper and Calder 1990). *Thelymitra media* and *T. aristata*, which Jones (1981) observed being visited by bees, also have impressive displays. *Thelymitra antennifera* is somewhat exceptional in that it has large, brightly coloured flowers, but there are only a few per inflorescence. The low numbers per inflorescence may be compensated by the mass flowering of many plants in large colonies in this species.

Many outcrossing species of *Thelymitra* emit sweet odours, which may enhance their attractiveness to nectar- or pollen-feeding insects. Expanded flowers of *T. megcalyptra* give off a strong, sweet fragrance similar to that of *Lavandula* (Lamiaceae) and *Syringa* (Oleaceae) according to Bernhardt and Burns-Balogh (1986*a*) and Backhouse and Jeanes (1995). *Thelymitra antennifera* is said to smell like a tea rose (Dafni and Calder 1987) or lemon-like (Jones 1988; Hoffman and Brown 1992; Backhouse and Jeanes 1995). *Thelymitra epipactoides* produces a sweet odour when fully expanded (Bates and Weber 1990; Cropper and Calder 1990) as does *T. aristata* (D. L. Jones, unpublished). *Thelymitra macrophylla* Lindl. and several of its near relatives in Western Australia are strongly scented (Hoffman and Brown 1992) with sour fragrances (D. L. Jones, unpublished). *Thelymitra ixioides* is exceptional, having no odour detectable by humans (Sydes and Calder 1993).

The opening of the corolla of outcrossing *Thelymitra* species in response to warmth and humidity (Ulherr 1970*b*) also varies greatly among species. Sunny, clear days with temperatures above 20°C are required to open the flowers of *T. megcalyptra* fully (Bernhardt and Burns-Balogh (1986*a*). Opening occurs between 08:30 and 10:30 and closing between 14:30 and 16:00. *Thelymitra antennifera* opens between about 09:00 and 16:00 on humid, sunny days with temperatures above 23°C (Dafni and Calder 1987). *Thelymitra epipactoides* flowers open with 20–28°C and 51–56% relative humidity and close at dusk (Cropper and Calder 1990). *Thelymitra ixioides* opens under cooler conditions than most other species, from 14–32°C and relative humidities of 30%–78% (Sydes and Calder 1993). Dafni and Calder observed that pollinator activity is confined to conditions of temperatures above 22°C, humidity above 65%, and low wind velocity, which correspond to those favouring flower opening.

Cheeseman (1881) suggested that *Thelymitra* flowers close in adverse weather to protect the pollinia from rain. He observed that if rain enters the column the friable pollinia of *T. longifolia* are often washed into 'a wet pulpy mass at the bottom of the recess behind the stigma'. However, this should not apply to obligately entomogamous species, which have strongly coherent pollinia. Nevertheless, closure would serve to protect the column from attack by herbivorous insect larvae and other threats.

Insects recorded visiting *Thelymitra* flowers are mainly native bees, and it seems clear that *Thelymitra* is adapted primarily for bee pollination (Jones 1981; Bernhardt and Burns-Balogh 1986*a*; Dafni and Calder 1987; Cropper and Calder 1990; Sydes and Calder 1993). Other recorded insects bearing pollinia include introduced hoverflies and a native sawfly. One female of each of two species of the native bee *Lasioglossum* subgenus *Chilalictus* were the only insects caught bearing pollinia of *T. megcalyptra* (as *T. nuda*) (Bernhardt and Burns-Balogh 1986*a*). Insects found with the pollinia of *T. antennifera* included seven specimens of a species of native *Lasioglossum* (*Chilalictus*), six of the introduced hoverfly (*Syrphus damastor*), and four of the native pergid sawfly, *Eurys* sp. (Dafni and Calder 1987). Of five insect species that visited flowers of *T. epipactoides* only one, females of a species of native halictid bee in the genus *Nomia* carried pollinaria and effected pollination (Cropper and Calder 1990). The others were a *Lasioglossum* (subgenus *Parasphecodes*) bee, two species of *Exoneura* bees, and a blowfly, *Calliphora stygia*, all of which carried pollen grains of *T. epipactoides.* Sydes and Calder (1993) reported two species of native bees in the genera *Exoneura* and *Lasioglossum* with pollinaria of *T. ixioides* and observed pollination by *Lasioglossum.* David L. Jones (unpublished) observed a halictid bee, *Lasioglossum* (*Chilalictus),* gathering disaggregated autogamous pollen of *T. cyanea* into the scopae on its hind legs. Although many syrphids visited flowers of *T. ixioides*, none removed pollinaria or effected pollination (Sydes and Calder 1993).

All the pollinators and suspected pollinators of *Thelymitra* so far identified are polyphagous nectar feeders and/or polylectic pollen gatherers that visit a wide range of other co-flowering species, as revealed by studies of their pollen loads. Females of the two *Lasioglossum* (*Chilalictus*) species with pollinaria of the blue-flowered *T. megcalyptra* also carried the pollen of Asteraceae, monocots and legumes (Bernhardt and Burns-Balogh 1986*a*). The bees attempted to 'buzz' the post-anther lobes and scrape the brushes of the lateral lobes and were also observed moving between *T. megcalyptra* and various nectarless, buzz-pollinated Hemerocallidaceae. Bernhardt and Burns-Balogh (1986*a*) concluded that *T. megcalyptra* is a mimic of blue and purple species with poricidal anthers.

Dafni and Calder (1987) showed that insects bearing the pollinia of the yellow-flowered *T. antennifera* also carried the pollen of co-flowering species with yellow or white corollas, particularly *Hibbertia* (Dilleniaceae), *Goodenia* (Goodeniaceae), and *Helichrysum* (Asteraceae). They concluded that *T. antennifera* imitates yellow flowers and that the fine yellow hairs on the column hood mimic pollen, which insects attempt to gather.

By contrast with *T. megcalyptra* and *T. antennifera*, *T. epipactoides* flowers are uniquely coloured and do not appear to mimic any particular species or flower guild (Cropper and Calder 1990). Rather, *T. epipactoides* appears to exhibit 'non-model mimicry' (Dafni 1986) or deception based on the innate search strategies of certain insects (Cropper and Calder 1990). Pollen present on the *Nomia* pollinators and other visitors to *T. epipactoides* came from flowers with a wide variety of morphology and colours, i.e. blue, purple, yellow, white, pink, and red. This indicates that *T. epipactoides* has evolved a generalist floral image encompassing the stimuli of many floral types.

'Non-model mimicry' was also proposed by Sydes and Calder (1993) as the pollination strategy of *T. ixioides.* In this case the pollen found on the *Exoneura* and *Lasioglossum* pollinators, and on the stigma of *T. ixioides*, was mainly from white flowers (*Leptospermum*; Myrtaceae) and yellow flowers (*Hibbertia* [Dilleniaceae] and *Acacia* [Fabaceae]), whereas *T. ixioides* is blue with darker blue spots. There were few other blue/purple species in the communities studied, and these were not the main species visited by the pollinators of *T. ixioides.*

Outcrossing species of *Thelymitra* generally have low pollination percentages. Cheeseman (1881) found only 3.1% of *T. longifolia* flowers in New Zealand had their pollinaria removed by insects, and 1.3% were pollinated. Bernhardt and Burns-Balogh (1986*a*) found 31.4% of *T. megcalyptra* flowers had the pollinaria removed but provided no estimate for pollinations. However, they noted that many flowers without pollinaria had fragments of pollinia on their stigmas and that 12 flowers also had pollinaria on the perianth after apparently being removed by bees from their bodies. Pollinaria removal and pollination percentages varied greatly among six populations of *T. antennifera* (Dafni and Calder 1987). Removals varied from 3.0%–26.0% and depositions from 0.3%–15.0% with a mean of 3.2%. Dafni and Calder (1987) concluded that the pollination in *T. antennifera* was negatively related to population density, such that the rate of pollination tends to be low at high flower densities and vice versa, but the data are limited. Cropper *et al.* (1989) found that coastal populations of *T. epipactoides* in Victoria were not pollinated during 1985 or 1986, whereas 35% of flowers at an inland site were pollinated in 1985. At two Victorian sites studied by Sydes and Calder (1993), pollinaria were removed from 49% and 64% of *T. ixioides* flowers, and 21% and 28% were pollinated, respectively, which are comparatively high levels. The factors affecting the pollination success of *Thelymitra* are unclear, and detailed ecological studies are needed on a greater number of populations over several seasons for each outcrossing species.

The relatively low rates of pollination in *Thelymitra* probably relate to the deception strategies of the genus. Bees and other insects may learn to avoid deceptive flowers (Bernhardt and Burns-Balogh 1986*a*). Some species of *Thelymitra* exhibit considerable variation in floral coloration or patterns (Burns-Balogh and Bernhardt 1988), which may slow the learning process. *Thelymitra epipactoides* exhibits substantial variation in corolla colour (Cropper and Calder 1990), and *T. ixioides* also exhibits some variation in the intensity of its blue coloration (some forms are even pink) and in the density of spotting on the perianth. Sydes and Calder (1993) suggested that the absence of a detectable odour in *T. ixioides* may also help reduce avoidance learning. Other highly variable species include *T. variegata* and *T. spiralis* (Lindl.) F. Muell. (Burns-Balogh and Bernhardt 1988; Hoffman and Brown 1992). However, some species, such as *T. antennifera*, show little variation (Dafni and Calder 1987).

Burns-Balogh and Bernhardt (1988) postulated that differential placement of pollinia on discrete areas of pollinator's bodies contributes to reproductive isolation among *Thelymitra* species, along with the exploitation of different groups of specialist oligolectic insects. However, there is little evidence of differential placement of pollinaria on the pollinators of outcrossing species. Most pollinators pick up the pollinaria on the last few segments of the abdomen, including those of *T. media* and *T. aristata* (Jones 1981), *T. megcalyptra* (Bernhardt and Burns-Balogh 1986*a*), *T. epipactoides* (Cropper and Calder 1990), and *T. ixioides* (Sydes and Calder 1993). The only fully documented exception is *T. antennifera*, in which pollinaria are placed on the mouthparts or abdomen (Dafni and Calder 1987). The claim by Burns-Balogh and Bernhardt (1988) that pollinaria are picked up on the ventral thorax of *Lasioglossum* species from *T. cyanea* (as *T. venosa*) requires confirmation. It is based on a photograph by R. Bates (reproduced in Bates and Weber 1990) in which the pollen placement is not clear; it seems more likely to be attached to the ventral abdomen or a leg and may be pollen gathered from other flowers. The identity of the bee is not given. In addition, *T. cyanea* is autogamous; the pollinia are not attached to the viscidium and cannot be removed as a unit (Rogers 1913; Jones 1971). Indeed, D. L. Jones (unpublished) has observed *Lasioglossum* (*Chilalictus*) bees gathering pollinia fragments on *T. cyanea* and storing them in the scopae on the hind legs. In the process of doing this, pollen was spread over the head and thorax.

Records of natural hybrids are relatively frequent in *Thelymitra* (McAlpine 1978; Bates 1985*a*; Clements 1989; Bates and Weber 1990), indicating that reproductive isolation between some species is incomplete. It appears that the use of polylectic pollinators, the relative lack of differential placement of pollinaria on insects, overlapping flowering periods, and weak postpollination barriers are contributing factors. Whereas many of the putative hybrids are among outcrossing species as would be expected, they also occur among outcrossing and predominantly autogamous species (Bates 1985*a*; Burns-Balogh and Bernhardt 1988). Pollen transfer may occur when pollinia are placed on the stigma of an autogamous flower or when fragments of pollen are picked up on the bodies of insects from the stigma of autogamous flowers and transferred to outcrossing species. The transfer of pollen from outcrossing flowers to the stigma of autogamous flowers would seem most likely, but the limited observations indicate the reverse. In the case of the hybrid *Thelymitra* × *truncata* studied by McAlpine (1978), the hybrid plants were growing with the outcrossing parent, *T. ixioides*, rather than with the autogamous parent, *T. pauciflora*, some distance away, indicating that the pollen was transferred from the autogamous to the outcrossing flowers and the resulting seed fell near the female parent.

Bates (1985*a*) asserted that most hybrids between outcrossing and autogamous species have the outcrossing species as female parent, but documentary evidence is not provided. If true, one possible explanation is that autogamous species tend to be common, and almost all their flowers have self-pollen on their stigmas so that visitors would have a high probability of picking up fragments of pollinia if they contact the stigma. Molloy and Dawson (1998) reported that insects can transfer pollen from autogamous *Thelymitra* species when their flowers open on warm sunny days. Bates (1984*b*) suggested syrphid flies may be the main vectors of pollen from autogamous species to other taxa. Syrphids may attempt to drink stigmatic fluid and collect pollen in the process (Burns-Balogh and Bernhardt 1988).

Bates (1985*a*) concluded that hybridization among outcrossing species is limited by differences in flowering times, perianth colour, and column structure. He reported that *T. antennifera* and *T. megcalyptra* (as *T. nuda*) often occur together, but *T. antennifera* tends to flower earlier, has yellow rather than blue flowers, and has different column ornamentation, which would attract different pollinators. Bates' contention is partly supported by the work of Bernhardt and Burns-Balogh (1986*a*) on *T. megcalyptra* and of Dafni and Calder (1987) on *T. antennifera*. Both *Thelymitra* species are pollinated by unidentified species of *Lasioglossum* (subgenus *Chilalictus*) bees, although a species of *Eurys* (Pergidae) and hoverflies, *Syrphus damaster*, may also pollinate *T. antennifera*. The key differences are that insects attracted to *T. antennifera* are polylectic on the guild of yellow-flowered plants whereas those visiting *T. megcalyptra* primarily visit the guild of blue/purple-flowered species. There is also a difference in the placement of pollinaria: on the mouthparts and frontal abdomen on visitors to *T. antennifera* and on the dorsal rear of the abdomen in *T. megcalyptra*. Nevertheless, occasional hybrids among *T. antennifera* and taxa related to *T. megcalyptra* have been reported in Western Australia (Bates 1985*a*). However, no evidence of hybridization was found at a locality in Victoria where the two occur together (Bernhardt and Burns-Balogh 1986*a*).

Introgression following hybridization seems to be rare. Few examples of hybrid swarms have been reported, and hybrids are generally found at low frequencies among the parents (Bates 1985*a*; Molloy and Dawson 1998). The population of *T.* × *truncata* studied by McAlpine (1978) contained apparent backcross individuals to *T. ixioides*, which McAlpine considered were equivalent to *T. merraniae* Nicholls. On the other hand, some hybrids are sterile, preventing introgression, such as the Australian *T.* × *irregularis*, the hybrid between *T. ixioides* and *T. carnea*, and the New Zealand *T.* × *dentata*, the hybrid between *T. pulchella* Hook.f. and *T. longifolia* J. Forst.& G. Forst. (Molloy and Dawson 1998; McCrae and Molloy 1998). These sterile hybrids have chromosome numbers intermediate between those of their two parents.

Recent studies in New Zealand indicated that many species have arisen in *Thelymitra* through natural hybridization and chromosome addition to give self-perpetuating amphidiploids (Molloy and Dawson 1998). Chromosome counts of *Thelymitra* in New Zealand produced a wide range from 26 to 84, but there was no obvious polyploid series. Many of the taxa have an intermediate appearance between other common species, particularly in column morphology, indicating hybridization is involved. As an example, *T. pulchella* with a chromosome number of 66 is considered to have arisen from hybridization of *T. longifolia* and *T. cyanea* with counts of 26 and 40, respectively. Similarly, *T. decora* with a chromosome count of 54 is thought to be derived from *T. ixioides* and *T. longifolia* with counts of 28 and 26, respectively (Molloy and Dawson 1998), a conclusion supported by isozyme studies (Peakall and Molloy 1998). Four extant amphidiploids are thought to have emerged in New Zealand and many others in Australia, at least four of which have dispersed to New Zealand (Molloy and Dawson 1998). The mechanism of pollen transfer to create such amphidiploid hybrids is unknown but is fundamental to an understanding of the evolution of *Thelymitra.* **(CCB)**

Uses

Thelymitra species are grown as ornamentals by specialist growers. Maoris ate the tubers of New Zealand species. **(DJ)**

Cultivation

Thelymitra is a genus with colourful flowers but frustrating in that the flowers will only open on warm to hot and usually humid days.

Mix: basic, well drained. Light: maximum light to not less than 25% shade. Watering: autumn to late spring. Flowering: mainly in spring. Mature plants flower well. Propagation: some species are colony-formers, e.g. *T. antennifera* (Lindl.) Hook.f. (multiplication rate on average ×2), whereas other species will sometimes produce a second tuber if the plants are large enough, e.g. *T. mucida* Fitzg., *T. epipactoides* F. Muell. They lend themselves to tuber removal or can be propagated from seed sown around the parent plant. **(HR)**

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C. TRIBE ORCHIDEAE

Tribe **Orchideae.** Dressler and Dodson, *Ann. Missouri Bot. Gard.* **47**, 25–67 (1960).

Tribe *Ophrydeae* Lindl., *Coll. Bot. App.* (1826). Type: *Ophrys* L.

Tribe *Gymnadenieae* Endl., *Fl. Poson.*, 162 (1830). Type: *Gymnadenia* R.Br.

Tribe *Habenarieae* Dunsterv. & Garay, *Venez. Orch. Ill.*, **2**, 28 (1961). Type: *Habenaria* Willd.

Tribe *Huttonaeae* Szlachetko, *Fol. Geobot. Phytotax.*, **26**, 326 (1991). Type: *Huttonaea* Harv.

Description

Terrestrial or rarely epiphytic *plants* usually with root tubers, less commonly rhizomatous, rarely mycotrophic with leaves reduced to colourless sheaths. *Tubers* ovoid, spherical, ellipsoidal or cylindric-fusiform, solitary or in clusters, hairy or glabrous, sometimes borne on short to long stolons or root-like stolons. *Leaves* spirally arranged, one to many, basal or caulescent, deciduous or rarely persistent for more than one year, often sheathing at the base, the lowermost one to several reduced to sheaths, the uppermost often bract-like, usually green, rarely spotted, rarely purple-spotted or shaded beneath. *Inflorescence* terminal, erect or arching, one–many-flowered, rarely secund; peduncle usually terete, glabrous or less frequently hairy or glandular; bracts linear, lanceolate, ovate or elliptic, sometimes cucullate, usually glabrous and green. *Flowers* small to large, usually resupinate, often showy, green, white, yellow, pink, purple or red; pedicel usually short, often obscure. *Dorsal sepal* free or often adnate to the petals to form a hood over the column. *Lateral sepals* usually free, rarely adnate to the base of the column, lip, stigma lobes or rostellum. *Petals* entire or two-lobed, often porrect, sometimes adnate to the dorsal sepal. *Labellum* usually lowermost in flower, usually deflexed, entire, three- or five-lobed, less commonly bipartite, occasionally callose, usually spurred at the base; spur saccate, scrotiform, fusiform, clavate or cylindrical, rarely fused to the ovary. *Column* basifixed, rarely adnate to the other floral

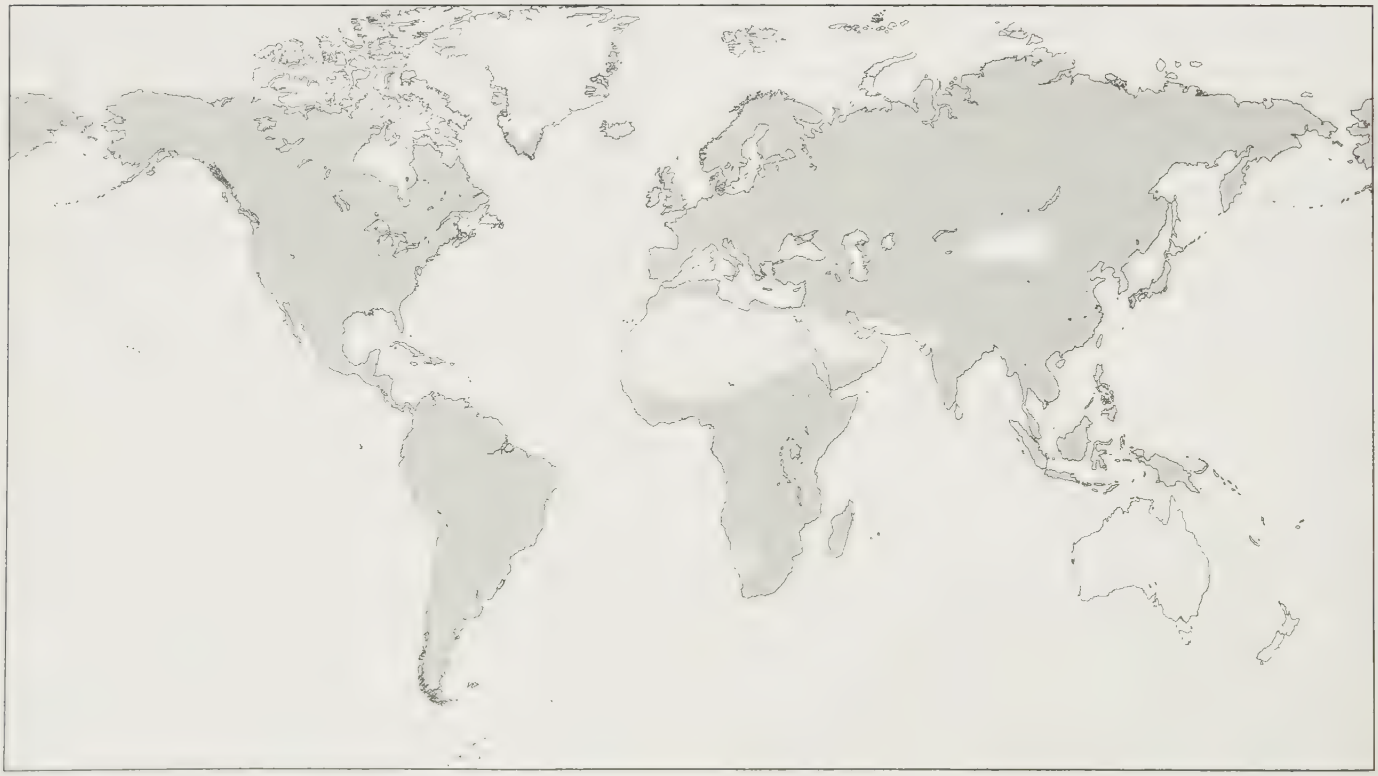

Fig. C.1. Distribution map of Orchideae.

segments at the base, erect or decumbent; anther bilocular, locules either adnate or separated on a more or less broad connective; pollinia two or four, sectile, attached by short to elongate caudicles to one or two viscidia; lateral appendages (often referred to as staminodes or auricles) two, usually present, sessile or stalked, usually shorter than the column, rarely filiform and as long as or longer than the column; stigma entire or two-lobed, sessile or stalked, concave to convex; rostellum usually three-lobed, sometimes obscure, the mid-lobe erect, lying between or in front of the anther loculi, the side lobes short to long, porrect, rarely incurved or upcurved. *Ovary* distinct, glabrous or less frequently hairy or glandular. **(PC)**

Distribution (Fig. C.1)

A tribe comprising two subtribes, about 62 genera and about 1800 species, well represented in northern temperate and tropical areas of both the Old and New Worlds, and particularly in the Afro-Madagascan region. Four endemic genera are found in Madagascar, three in Africa, and five in Asia. Only *Habenaria* species are found in tropical America. **(PC)**

Anatomy

Orchideae have been the subjects of extensive anatomical studies in the last two centuries from both developmental and comparative approaches. The history of developmental research to determine the morphological and anatomical nature of the organs of Orchidoideae has been outlined and interpreted elsewhere (Pridgeon and Chase 1995) with respect to Diurideae, but similar structures such as root tubers and droppers (or 'sinkers') also occur in Orchideae (Stern 1997 *a*, *b*) and Diseae (Kurzweil *et al.* 1995). Comparative studies of Orchideae are included in the comprehensive works of Möbius (1886, 1887), Dietz (1930), Solereder and Meyer (1930), Williams (1979), Rasmussen (1981), and Porembski and Barthlott (1988). These have been summarized and supplemented with new data by Stern (1997*a*, *b*). Freudenstein and Rasmussen (1999) used several anatomical characters such as presence of root tubers and velamen in their phylogenetic study of Orchidaceae, which showed among other things that Orchidoideae *sensu* Dressler (1993) is paraphyletic.

Anatomical similarities among Orchidinae and Habenariinae are presented here, based fundamentally on the papers by Stern (1997*a*, *b*) but also N. H. Williams (1979), Rasmussen (1981), and Møller and Rasmussen (1984). Peculiarities are noted for some taxa.

Leaf

SURFACE

Hairs absent, except unicellular, attenuate, sharp-pointed hairs on both surfaces *of Holothrix villosa* Lindl. and unicellular, blunt-tipped hairs in *Platanthera dilatata* (Pursh) Lindl. ex Beck. Staudermann (1924) reported unicellular hairs in *Holothrix orthoceras* Rchb.f. as well. Epidermis: cells polygonal except elongate abaxially in some species of *Anacamptis*, *Barlia*, *Galearis*, *Habenaria*, *Ophrys*, *Orchis*, and *Platanthera* and elongate on both surfaces in some species of *Anacamptis*, *Gymnadenia*, *Orchis*, *Platanthera*, and *Serapias*. Anticlinal walls curved to straight, occasionally lobed in some species. Stomata abaxial, except on both surfaces in several species of *Platanthera*; anomocytic (occasionally tetracytic), generally circular, greatest length/width range in *Galearis spectabilis* (L.) Raf. (108/79 μm), *Habenaria rhodocheila* Hance (85/65 μm), and *Stenoglottis longifolia* Hook.f. (88/65 μm).

TRANSECTION

Cuticle smooth to rugulose, less than 2.5 μm thick, except 7.5–12.5 μm thick adaxially and up to 25 μm thick abaxially in *Ophrys tenthredinifera* Willd. Epidermis: adaxial cells mostly anticlinal, abaxial cells anticlinal to isodiametric, some periclinal. Stomata superficial but slightly raised in *Brachycorythis macrantha* (Lindl.) Summerh., *Cynorkis fastigiata* Thouars, *Habenaria odontopetala* Rchb.f., *Habenaria rhodocheila*, *Holothrix villosa*, *Ophrys speculum* Link, and *Serapias vomeracea* (Burm.f.) Briq. Substomatal chambers small to moderate. Mesophyll: chlorenchyma homogeneous, with crystalliferous idioblasts. In some species of *Platanthera* large lacunae occur in the vicinity of the midvein. Vascular bundles collateral. The largest vascular bundles of some species of *Platanthera* extend from epidermis to epidermis.

Silica bodies in stegmata, sclerenchyma absent.

Stem

TRANSECTION

Hairs absent. Cuticle less than 2.5 μm thick. Epidermis: cells isodiametric to periclinal, mostly anticlinal in *H. rhodocheila*, thickened and rugulose in *Platanthera cristata* (Michx.) Lindl. Stomata absent, except occasional in *H. odontopetala* and frequent in *P. cristata*. Cortex: 3–14 cells wide depending on species, with large and numerous intercellular spaces. Endodermis: present in *Holothrix villosa*, bearing casparian strips. Ground tissue comprises an outer layer of generally thick-walled living cells and an inner layer of thin-walled living cells with collenchymatous thickenings. Vascular bundles collateral, scattered or in two series (e.g. *H. villosa*). Möbius (1886) reported a pericyclic sclerenchymatous ring continuous with vascular bundles in aerial parts of the stem in *Platanthera bifolia* (L.) Rich. Crystals: raphide bundles in *B. macrantha*. Silica bodies in stegmata and sclerencnyma are absent.

Tuber

TRANSECTION

Hairs unicellular, bulbous-based. Simple epidermis present in *Platanthera* and *Dactylorhiza fuchsii* (Druce) Soó. Velamen in other species examined 1– 5-layered, pitted or not, cells anticlinal or periclinal. Spiral thickenings occur in velamen cells of *Holothrix secunda* Rchb.f. Exodermis (absent in *Platanthera and D. fuchsii*): cells thin-walled, isodiametric to periclinal, dead cells with scalariform bars. Ground tissue either assimilatory with cruciate starch grains or else dead and storing water and/or mucilage. Mucilage cells present in some species, the contents refracting polarized light. Cortex of *Stenoglottis* species with assimilatory cells and larger, water-storing cells but lacking mucilage cells. Coronal cells with thick walls surround the endodermis in some species. Endodermis (either in central vascular cylinder or meristeles) single-layered, with obvious casparian strips. Pericycle single-layered. Stele undissected (11–65 arch in *Habenaria*, 6–8 arch in *Stenoglottis*; Sasikumar 1975; Stern 1997*a*) or else a series of meristeles scattered in the ground tissue (1–6 arch surrounded by one-layered endodermis and pericycle as above; Ogura 1953; Sasikumar 1975; Stern 1997*a*)

Root

TRANSECTION

Hairs unicellular. Simple epidermis (possibly velamentous in *Holothrix villosa*). Velamen 1–4-layered in *Cynorkis*, *Bonatea*, and *Stenoglottis*, as well as several other *Habenaria* species, without helical thickenings (Sasikumar 1975; Porembski and Barthlott 1988; Stern 1997*a*). Exodermis (in those species with velamen): dead cells thin-walled, the cell walls with scalariform bars. Cortex 4–15 cells wide, the middle layers with fungal hyphae and pelotons. Endodermis single-layered with casparian strips. Pericycle 1–3-layered depending on species. Stele 4–18 arch. Pith parenchymatous, occasionally with starch grains. Two steles, 5–6-arch, occur in *Habenaria distans* and three coalescent steles (3-, 2-, and 3-arch) in *H. monorrhiza*. A few isolated tracheary elements occur in the pith of *Stenoglottis longifolia*.

Dropper/Root-like stolon

Ogura (1953) described the stelar system of the 'stoloniferous root'or 'stalk' of several species of *Platanthera*, *Habenaria*, *Pecteilis*, and *Herminium*. Apart from his observations on the 'polysteles' (correctly meristeles) of the organs, little is known of their structure in Orchideae, but fundamental organization is probably similar to that in Diseae and Diurideae. **(AP)**

Palynology

The morphological heterogeneity of Orchideae pollen indicates that there are several characters of promising systematic utility, chiefly relating to sculpturing. Specific descriptions of ultrastructural observations from the literature are provided under generic headings. **(AP)**

Cytogenetics

A vast amount of literature has accumulated on the taxonomy and cytology of Orchideae. However, no detailed investigation has been made of the morphology of chromosomes of Orchideae.

Previous cytological studies have determined the chromosome numbers of numerous species of this group (Table C.2; Heusser 1938; Vermeulen 1947, 1972; Kliphuis 1963; Gadella and Kliphuis 1963; Vaucher 1966; Federov 1969; Bergen 1969; Löve and Simon 1968; Löve and Kjellqvist 1973; Sundermann 1973; Greilhuber and Ehrendorfer 1975; Scrugli *et al.* 1976; Sundermann and Von Der Bank 1977; Scrugli 1977, 1978, 1982; Del Prete 1977, 1978; Del Prete and Giordani 1978; Hautzinger 1978; Mazzola *et al.* 1982; Moore 1973, 1974, 1977; Natarajan 1978; Del Prete and Conte 1979; Tanaka and Kamemoto 1980; Soó 1980*a*, *b*; Corrias 1983; Cauwet-Marc and Balayer 1984, 1986; Bianco *et al.* 1987; Capineri and Rossi 1987; Medagli *et al.* 1991).

Recently, a more thorough examination of karyotype morphology was performed by D'Emerico *et al.* (1990, 1992, 1993, 1996*b*). Heterochromatin patterns were also studied in representative taxa of *Anacamptis* (D'Emerico *et al.* 1996*b*).

Chromosome numbers

Four basic chromosome numbers occur in Orchideae (Table C.1). This group is characterized by diploid chromosome numbers between $2n = 28$ and 42. These high chromosome numbers indicate a palaeo-polyploid origin and may have been derived from basic numbers $x = 6$ or $x = 7$ (Greilhuber and Ehrendorfer 1975), but are typical of all Orchidaeae, not only Orchideae.

Table C.1. Principal basic chromosome numbers in representative Orchideae

$x = 16$	$x = 18$	$x = 20$	$x = 21$
Anacamptis Rich. (including former *Orchis morio* group)	*Anacamptis* Rich. (including former *Orchis morio* group)	*Dactylorhiza* Neck. ex Nevski (including *Coeloglossum* Hartm.)	*Amerorchis* Hultén
	Barlia Parl.	*Gymnadenia* R.Br. (including *Nigritella*)	*Amitostigma* Schltr.
	Himantoglossum C.Koch		*Chamorchis* Rich.
	Ophrys L.		*Galearis* Raf.
	Serapias L.		*Habenaria* Willd.
			Neotinea Rchb. (including former *Orchis tridentata* group)
			Orchis L. (including *Aceras* R.Br.)
			Platanthera Rich.
			Pseudorchis Ség.
			Traunsteinera Rchb.

Table C.2. Chromosome numbers and karyotype formulae in species and subspecies of Orchideae from the literature

Taxon	Somatic chromosome number (from literature)	Karyotype formula
Amerorchis rotundifolia (Banks) Hultén	42 (Löve and Löve 1981)	
Amitostigma gracile Hinaran	42 (Tanaka 1965)	
Anacamptis boryi (Rchb.f.) R. M. Bateman, Pridgeon & M. W. Chase	36 (Wollin 1972)	
Anacamptis champagneuxii (Barnéoud) R. M. Bateman, Pridgeon & M. W. Chase	36 (Cauwet-Marc and Balayer 1984)	
Anacamptis collina (Banks & Sol. ex Russel) R. M. Bateman, Pridgeon & M. W. Chase[1]	36 (D'Emerico *et al.* 1990, 1996b)	$14m+4m^{s}+8sm+4sm^{s}+6sm_{sc}$
Anacamptis coriophora (L.) R. M. Bateman, Pridgeon & M. W. Chase[1]	36, 36 + II B (Capineri and Rossi 1987)	
Anacamptis coriophora (L.) R. M. Bateman, Pridgeon & M. W. Chase subsp. *fragrans* (Pollini) R. M. Bateman, Pridgeon & M. W. Chase[1]	36 (D'Emerico *et al.* 1993, 1996*b*)	$10m+2m^{s}+2m_{sc}+14sm+6sm_{sc}+2st$
Anacamptis laxiflora (Lam.) R. M. Bateman, Pridgeon & M. W. Chase[1]	36 (Scrugli 1977; Bianco *et al.* 1991; D'Emerico *et al.* 1996*b*)	$24m+6sm+4sm^{s}+2sm_{sc}$
Anacamptis longicornu (Poir.) R. M. Bateman, Pridgeon & M. W. Chase[1]	36 (D'Emerico *et al.* 1996*b*)	$26m+4m^{s}+6sm$
Anacamptis morio (L.) R. M. Bateman, Pridgeon & M. W. Chase[1]	36 (D'Emerico *et al.* 1990, 1996*b*)	$20m+4m^{s}+4sm+6sm^{s}+2st^{s}$ $26m+4m^{s}+4sm+2sm^{s}$
Anacamptis palustris (Jacq.) R. M. Bateman, Pridgeon & M. W. Chase[1]	36 (D'Emerico *et al.* 1990, 1996*b*)	$16m+4m^{s}+2m_{sc}+12sm+2sm^{s}$
Anacamptis papilionacea (L.) R. M. Bateman, Pridgeon & M. W. Chase[1]	32 (D'Emerico *et al.* 1990, 1996*b*)	$10m+2m^{s}+8sm+6sm^{s}+4st+2st^{s}$ $16m+2m^{s}+10sm+2sm^{s}+2st$
Anacamptis papilionacea (L.) R. M. Bateman, Pridgeon & M. W. Chase subsp. *grandiflora* (Boiss.) Nelson[1]	32 (D'Emerico *et al.* 1996*b*)	$16m+10sm+4sm^{s}+2st^{s}$
Anacamptis pyramidalis (L.) Rich.[1]	36, 54, 63, 72 (Del Prete 1991; Bianco *et al.* 1991; D'Emerico *et al.* 1993)	$2n=36$: $20m+2m^{s}+6sm+8sm$
Barlia robertiana (Loisel.) W. Greuter[1]	36 (D'Emerico *et al.* 1992)	$26m+6m^{s}+4sm^{s}$
Brachycorythis helferi (Hook.f.) Summerh.	42 (Larsen 1966)	
Brachycorythis obcordata (Lindl.) Summerh.	42 (Mehra and Kashyap 1978)	
Chamorchis alpina (L.) Rich.[1]	42 (Engelskjoen and Knaben 1971)	
Cynorkis anacamptoides Kränzl.	28 (Thulin 1970)	
Dactylorhiza aristata (Fisch. ex Lindl.) Soó	40 (Löve and Simon 1968)	
Dactylorhiza coccinea (Pugsley) Averyanov	40 (Moore 1982)	
Dactylorhiza cruenta (O. F. Müller)	40 (Heusser 1938)	
Dactylorhiza elata (Poir.) Soó	80 (Moore 1982)	
Dactylorhiza foliosa (Verm.) Soó	40 (Sundermann and Wattke 1973)	
Dactylorhiza fuchsii (Druce) Soó	40 (Moore 1982)	
Dactylorhiza iberica (M. Bieb. ex Willd.) Soó	40 (Moore 1982)	
Dactylorhiza incarnata (L.) Soó subsp. *pulchella* (Druce) Soó	40 (Moore 1982)	
Dactylorhiza insularis (Sommier) Landwehr[1]	60 (Scrugli 1977; D'Emerico *et al.* 1992)	$24m+14m^{s}+20sm+2st$
Dactylorhiza lapponica (Laest.) Soó	80, 120 (Soó 1980*a*)	
Dactylorhiza latifolia (L.) Soó (= D. sambucina)	40 (Heusser 1938)	
Dactylorhiza maculata (L.) Soó	40, 60, 80 (Moore 1982)	
Dactylorhiza praetermissa (Druce) Soó	80 (Moore 1982)	

Table C.2. *(continued)*

Taxon	Somatic chromosome number (from literature)	Karyotype formula
Dactylorhiza romana (Sebast.) Soó[1]	40 (Bianco *et al.* 1987)	
Dactylorhiza saccifera (Brongn.) Soó[1]	40 (Cauwet-Marc and Balayer 1984)	
Dactylorhiza traunsteineri (Saut.) Soó	80 (Moore 1982)	
Dactylorhiza viridis (L.) R. M. Bateman, Pridgeon & M. W. Chase	40 (Capineri and Rossi 1987)	
Diplomeris hirsuta D. Don	42 (Mehra and Kashyap 1976)	
Galearis spectabilis (L.) Raf.	42 (Löve and Simon 1968)	
Gennaria diphylla (Link) Parl.	34, 40 (Scrugli 1978; Sundermann and von der Bank 1977)	
Gymnadenia archidueis-joannis (Teppner & Klein) Teppner & Klein	80 (Teppner and Klein, 1985)	
Gymnadenia buschmanniae (Teppner & Ster) Teppner & E. Klein[1]	100 (Teppner and Ster 1996)	
Gymnadenia carpatica (Zapal.) Teppner & E. Klein	40 (Teppner *et al.* 1994)	
Gymnadenia conopsea (L.) R.Br.[1]	40 (Cauwet-Marc and Balayer 1986)	
Gymnadenia corneliana (Beauv.) Teppner & E. Klein	40 (Gerbaud and Gerbaud 1996)	
Gymnadenia dolomitensis Teppner & E. Klein	80 (Teppner and Klein 1998)	
Gymnadenia gabasiana (Teppner & E. Klein) Teppner & E. Klein	40 (Teppner and Klein 1993)	
Gymnadenia lithopolitanica (Ravnik) Teppner & E. Klein	40 (Teppner and Klein 1985*a*)	
Gymnadenia miniata (Crantz) Hayek	80 (Teppner and Klein 1985*a*)	
Gymnadenia nigra (L.) Rchb.f.[1]	80 (Teppner and Klein 1985*a*)	
Gymnadenia odoratissima (L.) Rich.[1]	40 (Cauwet-Marc and Balayer 1986)	
Gymnadenia rhellicani (Teppner & E. Klein) Teppner & E. Klein[1]	40 (Teppner and Klein 1990)	
Gymnadenia stiriaca (K. Rech.) Teppner & E. Klein	80 (Teppner and Klein 1985*a*)	
Gymnadenia widderi (Teppner & E. Klein) Teppner & E. Klein	80 (Teppner and Klein 1985*b*)	
Habenaria acuifera Wall. ex Lindl.	42 (Mehra and Sehgal 1974)	
Habenaria aitchisonii Rchb.	42 (Mehra & Vij 1970)	
Habenaria arietina Hook.f.	28, 42 (Mehra and Bawa 1970; Sharma and Sarkar 1967)	
Habenaria aristata Hook.f.	42, 122 (Mehra and Vij 1970; Mehra and Sehgal 1974)	
Habenaria biermanniana King & Pantl.	42 (Mehra and Vij 1970)	
Habenaria commelinifolia Wall.	42 (Mehra and Kashyap 1978)	
Habenaria crassifolia Rich.	42 (Jorapur and Kulkarni 1980)	
Habenaria crenifera Lindl.	42 (Kulkarni and Jorapur 1979)	
Habenaria densa Wall.	44, 46, 48 (Mehra and Vij 1972; Mehra and Kashyap 1979)	
Habenaria dilatata Pursh	42 (Arora 1968))	
Habenaria edgeworthii Hook.f.	42, 84 (Mehra and Kashyap 1976; Arora 1968)	
Habenaria elegans (Lindl.) Boland	42 (Niehaus and Wong 1971)	
Habenaria ensifolia Lindl.	42 (Mehra and Bawa 1962)	
Habenaria fallax King & Pantl.	30, 42 (Mehra and Vij 1970; Mehra and Kashyap 1978)	
Habenaria geniculata D. Don	42, 84, 168 (Mehra and Vij 1970, 1972; Mehra and Sehgal 1974)	
Habenaria gibsonii Hook.	42 (Jorapur 1980)	

Table C.2. (*continued*)

Taxon	Somatic chromosome number (from literature)	Karyotype formula
Habenaria goodyeroides D. Don	42, 46 (Mehra and Vij 1970, 1972)	
Habenaria grandifloriformis Blatt. & McCann	44 (Jorapur and Kulkarni 1980)	
Habenaria graveolens Duthie	42 (Arora 1968)	
Habenaria josephii Rchb.f.	40 (Mehra and Kashyap 1978)	
Habenaria keyneana Lindl.	44 (Jorapur and Garg 1980)	
Habenaria khasiana Hook.f.	42 (Mehra and Sehgal 1974)	
Habenaria lacertifera Benth.	44 (Mehra and Sehgal 1974)	
Habenaria lawii Hook.f.	42 (Mehra and Kashyap 1978)	
Habenaria longicorniculata Graham	40 (Kulkarni and Jorapur 1979)	
Habenaria marginata Colebr.	42 (Mehra and Kashyap 1976)	
Habenaria miersiana Champ.	62, 64 (Miduno 1939; Mutsuura and Nakahira 1960)	
Habenaria ovalifolia Wight	44 (Jorapur 1980)	
Habenaria panchganiensis Santapau & Kapadia	42 (Jorapur and Kulkarni 1980)	
Habenaria pectinata Lindl.	42, 42+0–2B (Arora 1968; Mehra & Kashyap 1976)	
Habenaria plantaginea Lindl.	42, 126 (Arora 1968; Mehra and Vij 1970)	
Habenaria saccata Greene	42 (Niehaus and Wong 1971)	
Habenaria sparsiflora Wats.	42 (Niehaus and Wong 1971)	
Habenaria stenopetala Lindl.	42 (Singh 1981)	
Habenaria stenostachya Benth.	42+2B (Mehra and Sehgal 1974)	
Habenaria subpubens Rich.	44 (Jorapur and Garg 1980)	
Habenaria susannae R.Br.	42 (Mehra and Bawa 1970)	
Habenaria tridactylites Lindl.	42 (Mehra and Vij 1970)	
Habenaria viridis R.Br.	42 (Mehra and Vij 1970)	
Herminium angustifolium Benth.	38, 76 (Mehra and Bawa 1962; Mehra and Vij 1970)	
Herminium congestum Lindl.	40 (Mehra and Kashyap 1981)	
Herminium duthiei Hook.f.	40 (Mehra and Kashyap 1976)	
Herminium elisabethae (Duthie) Tang & Wang	42 (Mehra and Bawa 1970)	
Herminium fallax Hook.f.	34 (Mehra and Sehgal 1974)	
Herminium gramineum Lindl.	36, 40 (Arora 1968; Mehra and Kashyap 1978)	
Herminium jaffereyanum King & Pantl.	38 (Mehra and Bawa 1970)	
Herminium josephii Rchb.f.	38 (Mehra and Bawa 1970)	
Herminium lanceum (Thunb. ex Sw.) Vuijk	38, 42 (Arora 1971; Mehra and Sehgal 1980)	
Herminium monorchis (L.) Rich.	38, 40 (Heusser 1938; Kliphuis 1963; Vij and Gupta 1975)	
Herminium quinquilobium King & Pantl.	38 (Mehra and Bawa 1970)	
Himantoglossum adriaticum H. Baumann	36, 36 + 1B (Capineri and Rossi 1987; D'Emerico *et al.* 1993)	$20m+8m^{S}+8sm$

Table C.2. *(continued)*

Taxon	Somatic chromosome number (from literature)	Karyotype formula
Himantoglossum hircinum (L.,) Spreng.	36, 36 + 1B (Capineri and Rossi 1987; D'Emerico *et al.* 1990)	$24m+4m^{S}+2sm+6sm^{S}$
Neotinea maculata (Desf.) Stearn	42 (Cauwet-Marc and Balayer 1984	
Neotinea lactea (Poir.) R.M. Bateman, Pridgeon & M.W. Chase	42 (Scrugli 1977; D'Emerico *et al.* 1992)	$20m+8m^{S}+10sm+4sm^{S}$
*Neotinea tridentata** (Scop.) R.M. Bateman, Pridgeon & M.W. Chase subsp. *tridentata*	42, 42 + 1B (D'Emerico *et al.* 1990)	$22m+12m^{S}+6sm+2sm^{S}$
*Neotinea tridentata** (Scop.) R.M. Bateman, Pridgeon & M.W. Chase subsp. *commutata* (Tod.) R.M. Bateman, Pridgeon & M.W. Chase	84 (Mazzola *et al.* 1981)	
Neotinea ustulata (L.) R.M. Bateman, Pridgeon & M.W. Chase	42, 42 +1B (D'Emerico *et al.* 1990)	
Ophrys aesculapii Renz	36 (Soó 1980b)	
Ophrys apifera Huds.	36 (Greilhuber and Ehrendorfer 1975; Bianco *et al.* 1987)	
Ophrys apulica (O. & E. Danesch) O. & E. Danesch	36 (Bianco *et al.* 1987)	$16m+12sm+8sm^{S}$
Ophrys arachnitiformis Grenier & Philippe	36 (Scrugli 1977; Del Prete and Giordani 1987)	
Ophrys archipelagi Gölz & Reinhard	36 (Medagli *et al.* 1991)	$14m+4m^{S}+14sm+4sm^{S}$
Ophrys benacensis (Reisigl) O. & E. Danesch & Ehrendorfer	36 (Greilhuber and Ehrendorfer 1975)	
Ophrys bertoloniiformis O. & E. Danesch	36 (Greilhuber and Ehrendorfer 1975)	
Ophrys bertolonii Mor.	36 (Bianco *et al.* 1989a)	$12m+2m^{S}+16sm+4sm^{S}+2st^{S}$
Ophrys biscutella O. & E. Danesch	36 (Greilhuber and Ehrendorfer 1975)	
Ophrys bombyliflora Link	36 (Bianco *et al.* 1989b)	$24m+6m^{S}+4sm+2sm^{S}$
Ophrys candica (E. Nelson ex Soó) Bauman & Künkele	36 (Bianco *et al.* 1987)	
Ophrys chestermanii (J.J. Wood) Gölz & Reinhard	36 (Corrias 1983)	
Ophrys ciliata Biv.-Bern.[1]	36 (Scrugli 1977; Soó 1980b)	
Ophrys episcopalis Poir.	36 (Soó 1980b)	
Ophrys exaltata Ten.	36 (Del Prete and Giordani 1978)	
Ophrys fuciflora (F. W. Schmidt) Moench[1]	36 (Greilhuber and Ehrendorfer 1975)	
Ophrys fuciflora (F.W. Schmidt) Moench subsp. *gracilis* Büel & O. & E. Danesch	36 (Greilhuber and Ehrendorfer 1975)	
Ophrys fusca L.[1]	36, 72 (Greilhuber and Ehrendorfer 1975) Scrugli 1977; Bianco *et al.* 1989a)	$26m+2m^{S}+4sm+4sm^{S}$
Ophrys garganica O. & E. Danesch[1]	36 (Bianco *et al.* 1989b)	$18m+2m^{S}+10sm+6sm^{S}$
Ophrys incubacea Bianca[1]	36 (Bianco *et al.* 1989b)	$16m+12sm+8sm^{S}$
Ophrys insectifera L.[1]	36 (Greilhuber and Ehrendorfer 1975)	
Ophrys iricolor Desf.[1]	36 (Scrugli 1977)	
Ophrys lacaitae Lojac.[1]	36 (Mazzola *et al.* 1981)	
Ophrys lunulata Parl.	36 (Del Prete and Giordani 1978)	
Ophrys lutea Cav.[1]	36 (Scrugli 1977; Bianco *et al.* 1989b)	$22m+2m^{S}+6sm+6sm^{S}$
Ophrys mateolana Medagli, D'Emerico, Bianco & Ruggiero[1]	36 (Medagli *et al.* 1991)	

Table C.2. *(continued)*

Taxon	Somatic chromosome number (from literature)	Karyotype formula
Ophrys morisii (U. Martelli) Soó[1]	36	
Ophrys oestrifera M. Bieb.[1]	36 (Medagli *et al.* 1995)	
Ophrys oxyrrhynchos Tod.	36 (Mazzola *et al.* 1981)	
Ophrys oxyrrhynchos Tod. subsp. *celiensis* (O. & E. Danesch) Del Prete[1]	36 (Bianco *et al.* 1989a)	$16m+2m^S+12sm+4sm^S+2st^S$
Ophrys pallida Raf.	36 (Mazzola *et al.* 1981)	
Ophrys parvimaculata (O. & E. Danesch) Pauius & Gack[1]	36 (Bianco *et al.* 1987)	
Ophrys praecox (B. Corrias) J. & P. Devillers-Teschuren[1]	36 (Corrias 1983)	
Ophrys promontorii O. & E. Danesch[1]	36 (Greilhuber and Ehrendorfer 1975)	
Ophrys regis-ferdinandi (Renz) Buttler	36 (Soó 1980b)	
Ophrys scolopax Cav.[1]	36 (Greilhuber and Ehrendorfer 1975)	
Ophrys sicula Tineo[1]	36 (Bianco *et al.* 1989b)	$22m+2m^S+6sm+6sm^S$
Ophrys sipontensis Lorenz & Gembardt	36 (Greilhuber and Ehrendorfer 1975)	
Ophrys sphegodes Miller[1]	36 (Bianco *et al.* 1989a)	$22m+6sm+6sm^S+2st^S$
Ophrys tardans O. & E. Danesch[1]	36	
Ophrys tarentina Gölz & Reinhard[1]	36 (Bianco *et al.* 1987)	$20m+10sm+4sm^S+2st^S$
Ophrys tenthredinifera Willd.[1]	36 (Bianco *et al.* 1991)	$18m+6m^S+6sm+6sm^S$
Orchis anatolica Boiss.	42 (Sundermann and Wattke 1973)	
Orchis anthropophora (L.) All.[1]	42 (Scrugli 1977)	
Orchis brancifortii Biv.-Bern.	42 (Mazzola *et al.* 1981)	
Orchis ichnusae (Corrias) J. Devillers-Terschuren & P. Devillers-Terschuren[1]	42	
Orchis italica Poir.[1]	42 (Moore 1982; Bianco *et al.* 1991)	
Orchis mascula (L.) L.[1]	42 (Löve and Kjellqvist 1973; Scrugli *et al.* 1976)	
Orchis militaris L.[1]	42 (Moore 1982)	
Orchis patens Desf.[1]	84 (Hautzinger, 1978)	
Orchis pauciflora Ten.	42 (Del Prete 1977)	
Orchis provincialis Balb. ex Lam. & DC[1]	42 (Scrugli 1977)	
Orchis purpurea Huds.[1]	42 (Moore 1982)	
Orchis quadripunctata Cirillo ex Ten.[1]	42 (Corrias 1983)	
Orchis simia Lam.[1]	42 (Moore 1982)	
Orchis spitzelii Sauter	42 (Löve and Kjellqvist 1973)	
Pecteilis latilabris (Lindl.) Mitra	42 (Arora 1971)	
Pecteilis radiata Raf.	32, 48 (Miduno 1939, 1940)	
Peristylus goodyeroides Lindl.	28, 42, ca.44, 46 (Larsen 1966; Arora 1968; Mehra and Kashyap 1978)	
Peristylus gracilis Blume	42 (Larsen 1966)	
Peristylus lawii Wight	42, 46 (Jorapur and Garg 1980; Singh 1981)	
Peristylus plantagineus Lindl.	46 (Jorapur and Garg 1980)	

Table C.2. (*continued*)

Taxon	Somatic chromosome number (from literature)	Karyotype formula
Peristylus stenostachyus (Lindl.) Kränzl.	46 (Jorapur andGarg 1980)	
Peristylus stocksii Kränzl.	42, 46 (Jorapur and Garg 1980; Singh 1981)	
Peristylus xanthachlous Blatt. & McCann	46 (Jorapur and Garg 1980)	
Platanthera algeriensis Battandier & Trabat[1]	42	
Platanthera bifolia (L.) Rich.	42 (Cauwet-Marc and Balayer 1986)	
Platanthera chlorantha (Custer) Rchb.[1]	42 (Cauwet-Marc and Balayer 1986)	
Platanthera florentia Franch. & Sav.	42 (Yokota 1987)	
Platanthera hyperborea (L.) Lindl.	42, 84 (Dalgaard 1989)	
Pseudorchis albida (L.) A. & D. Löve	42 (Cauwet-Marc and Balayer 1986)	
Serapias apulica (Baumann & Künkele) P. Delforge[1]	36 (D'Emerico *et al.* 1990)	$4m+10m^s+8sm+10sm^s+2st+2st^s$
Serapias cordigera L.[1]	36 (Cauwet-Marc and Balayer 1986)	
Serapias lingua L.[1]	72 (Cauwet-Marc and Balayer 1986)	
Serapias neglecta De Not.	36 (Del Prete *et al.* 1980)	
Serapias nurrica Corrias	36 (Scrugli 1982)	
Serapias orientalis (Greuter) H. Baumann & Künkele	36 (Moore 1980)	
Serapias parviflora Parl.[1]	36 (Moore 1982; Bianco *et al.* 1990)	$8m+16m^s+6sm+6sm^s$
Serapias politisii Renz[1]	36 (Bianco *et al.* 1992)	$8m+8m^s+6sm+14sm^s$
Serapias vomeracea (Burm.f.) Briq.[1]	36 (D'Emerico *et al.* 1992)	$10m+10m^s+12sm+4sm^s$
Serapias vomeracea Briq. subsp. *laxiflora* Gölz & Reinhard[1]	36 (D'Emerico *et al.* 1992)	$6m+12m^s+14sm+4sm^s$
Stenoglottis longifolia Lindl.	36 (Tanaka 1964)	
Traunsteinera globosa (L.) Rchb.	42 (Moore 1982)	

[1] Confirmed data from analyses by D'Emerico *et al.* [2] Abbreviations: m = metacentric; sm = submetacentric; st = subtelocentric; t = telocentric; s = satellite; sc = secondary constriction.

Karyotype evolution in some Orchideae

The structural change of chromosomes in karyotype evolution is one of the most important aspects of the evolutionary process (Levitsky 1931; Stebbins 1971; Jones 1978). In this connection, a significant expression of chromosomal change affecting species is the alterations in chromosome structure and constitutive heterochromatin. The latter can be compared in different taxa to support taxonomic and phylogenetic correlation (Nagl 1979; Stergianou 1989; Pignone *et al.* 1994; D'Emerico *et al.*, 1996*b*). Moreover, numerous investigators suggested the role of heterochromatin in evolution and ecological adaptation (Vosa 1973, 1996, 1997; Miklos and Nankivell 1976; Loidl 1987; Bassi 1990, 1991; Stergianou 1989; Vosa and Stergianou 1990).

In Orchideae conspicuous differences in the karyotype morphology and constitutive heterochromatin have been found. In addition, correlation between the degree of karyotype asymmetry and heterochromatin content has been observed. Comparative karyological studies of *Anacamptis* species indicated certain differences that are often correlated with trends of specialization in the external morphology and ecological adaptation. Karyotype specialization has been observed in some *Anacamptis* species with $2n = 32$ or $2n = 36$ (Fig. C.2). In fact, *A. coriophora* and *A. papilionacea* are characterized by a more asymmetric karyotype and larger heterochromatin content than those of the *Anacamptis morio* group (Fig. C.3). A trend in the direction of a less asymmetrical karyotype and a corresponding decrease in constitutive heterochromatin has been observed in species of *Barlia* and *Himantoglossum.*

Evidence exists that alterations in the amount of heterochromatin can be induced by structural rearrangements (Bernard and Miklos 1979). In fact, the taxa with higher telomeric heterochromatin content and more asymmetrical karyotype should be more highly evolved than the species with less asymmetrical and heterochromatic karyotypes. In previous work an association of the

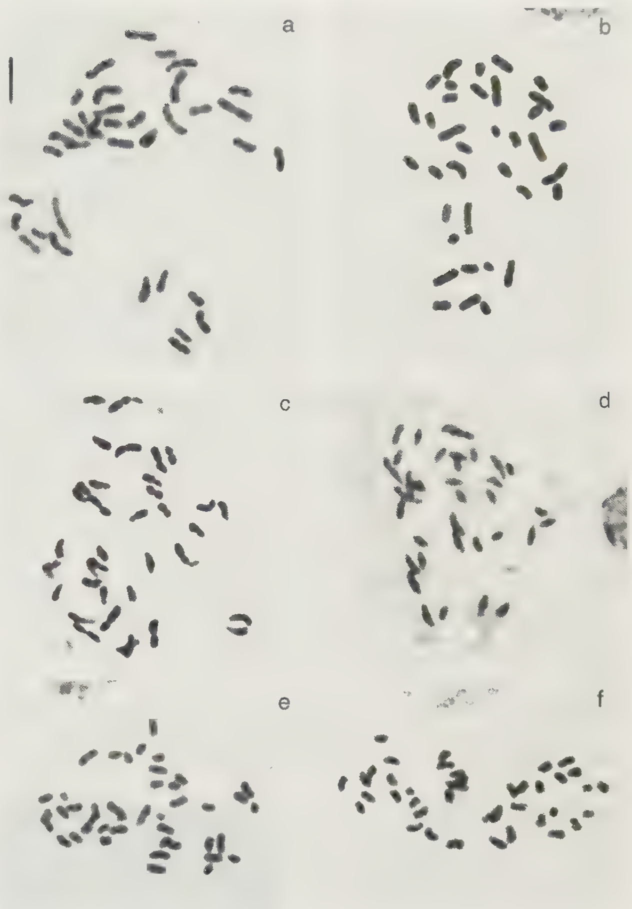

Fig. C.2. Feulgen-stained somatic metaphases in Orchidinae species. a. *Anacamptis morio*, $2n = 36$; b. *Anacamptis pyramidalis*, $2n = 36$; c. *Ophrys tarentina*, $2n = 36$; d. *Serapias vomeracea*, $2n = 36$; e. *Orchis italica*, $2n = 42$; f. *Dactylorhiza saccifera*, $2n = 40$. Scale bar = 5 μm (original by S. D'Emerico).

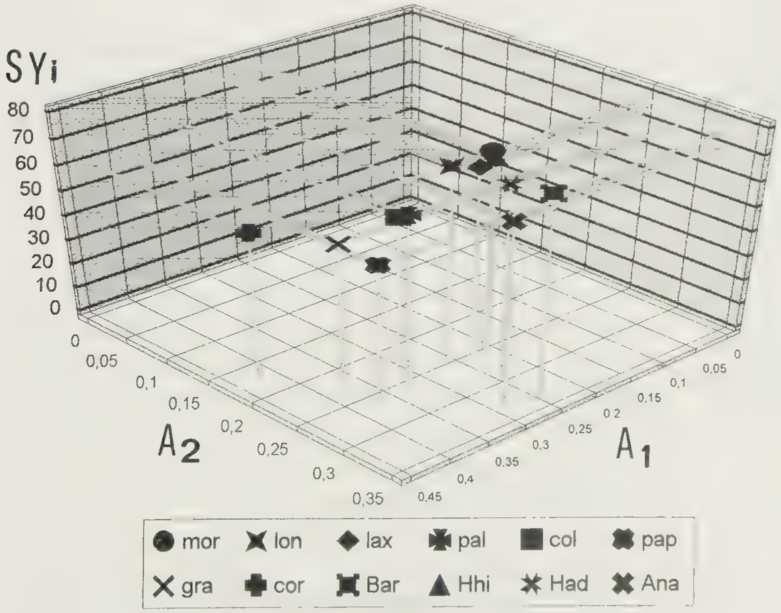

Fig. C.3. Scatter diagram of the values of A_1, A_2, and SYi of the karyotypes of the $2n = 32$, 36 *Anacamptis* species, *Barlia robertiana*, *Himantoglossum adriaticum,* and *H. hircinum.* A_1 measures the average position of the centromere in a karyotype; A_2 expresses the variation in chromosome lengths; SYi describes the average symmetry of the karyotype. Modified after D'Emerico *et al.* (1996). Code: mor = *Anacamptis morio*, lon = *A. longicornu*, lax = *A. laxiflora*, pal = *A. palustris*, col = *A. collina*, pap = *A. papilionacea*, gra = *A. papilionacea* subsp. *grandiflora*, cor = *A. coriophora*, bar = *Barlia robertiana*, Hhi = *Himantoglossum hircinum*, Had = *H. adriaticum*, Ana = *A. pyramidalis.*

heterochromatin content with evolutionary indicators has been observed in other orchids (Stergianou 1989; Vij 1989). In this connection, *Anacamptis coriophora* represents the remnant of a group of species that actually diverged from the other species of *Anacamptis*. On the other hand, karyomorphological and heterochromatin diversification in *A. papilionacea* provides some evidence bearing on the role of ecological versus genomic changes in microevolution.

In *Serapias* and *Ophrys* species, the heterochromatin amount seems to be related to karyotype asymmetry. Of considerable interest is the position of heterochromatin in the chromosomes of these species. C-banding shows the presence of constitutive heterochromatin at the centromeric regions of numerous chromosomes. *Serapias* species possess chromosomes containing a large amount of constitutive heterochromatin covering the centromeric area, whereas *Ophrys* species show thin centromeric heterochromatin (Fig. C.4; D'Emerico *et al.*, in preparation). A general similarity in the centromeric heterochromatin indicates that the above-mentioned genera are derived from a common ancestral stock. On the other hand, the chromosome complement of *Serapias* species is characterized by the presence of large centromeric heterochromatin (Fig. C.4). Bernard and Miklos (1979) reported some results indicating that increases in centromeric heterochromatin are generated when structural rearrangements occur in complement chromosomes. Our cytological data are in agreement with those reported by Bernard and Miklos (1979), and on this basis we can suggest that the *Serapias* group could be considered karyologically more recent that the *Ophrys* group.

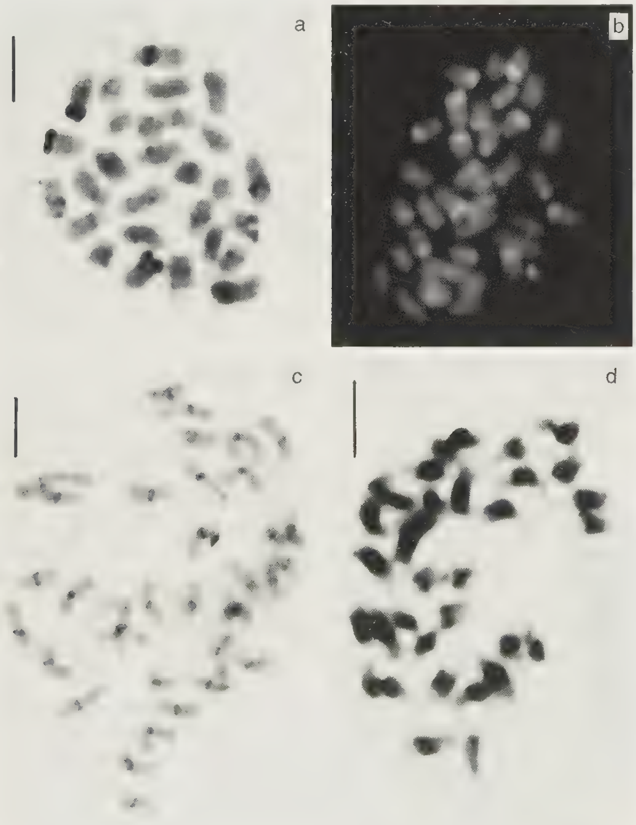

Fig. C.4. C-banding in some Orchidinae. a. *Anacamptis papilionacea*, somatic metaphase, Giemsa C-banded. b. *Anacamptis coriophora* subsp. *fragrans*, fluorochrome H33258-stained somatic metaphase. c. *Ophrys tenthredinifera*, somatic pro-metaphase, Giemsa C-banded. d. *Serapias vomeracea*, somatic pro-metaphase, Giemsa C-banded. Scale bar = 5 μm (original by S. D'Emerico).

Although substantial progress has been made in cytogenetical studies of subtribe Orchidinae, much remains to be understood mainly because of difficulties related to the small size of the chromosomes and/or complex karyotype structure. In these cases, the techniques of molecular cytogenetics will enable us to analyse karyotype morphology and localize DNA regions on chromosomes, particularly with the methods of *in situ* hybridization. **(SD)**

Phytochemistry

Phytochemical data are available for *Anacamptis, Barlia, Chamorchis, Dactylorhiza, Gymnadenia, Habenaria, Herminium, Himantoglossum, Neotinea, Ophrys, Orchis, Peristylus, Platanthera, Pseudorchis*, and *Serapias* (see separate entries). Flower anthocyanins in species of these genera and of *Neottianthe* and *Traunsteinera* were described by Strack *et al.* (1989). (**NV**, **RG)**

Phylogenetics

Previous phylogenetic studies of Orchideae

Thus far, morphological cladists have focused on broad-brush analyses of the entire orchid family. Dressler's (1993) rather character-depauperate scheme of the Orchideae and Diseae at subtribal level yielded a polytomy of the Orchidinae, Habenariinae, and Diseae. The genus-based phylogeny of Freudenstein and Rasmussen (1999) generated a fairly well-supported, derived Orchideae–Diseae clade, but no meaningful resolution among the four representative genera included (*Disa*, *Satyrium*, *Platanthera*, *Dactylorhiza*). Studies of allozymes (Schlegel *et al.* 1989; Rossi *et al.* 1994) and cpDNA RFLPs (Cozzolino *et al.* 1998) were weakened by sparse sampling of the triphyletic *Orchis s.l.* and/or suboptimal choice of outgroups.

Early molecular phylogenetic studies of Orchidaceae that included representative species of Orchideae used the plastid genes *rbcL* (Chase *et al.* 1994) and *ndhF* (Neyland and Urbatsch 1996). Kores *et al.* (1997) obtained strong jackknife support for monophyly of the Orchideae but no support for their preferred pectinate topology within the clade of (((*Satyrium*, *Disa*) *Habenaria*) *Orchis*). The next *rbcL* study of the Orchidaceae (Cameron *et al.* 1999) overturned all of the relationships inferred by Kores *et al.* to yield the topology (((*Satyrium*, *Platanthera*) *Habenaria*) (*Ophrys*, *Orchis*) *Disa*), albeit again without strong support for the internal nodes. Thus, the primary inference gained from plastid sequences is the monophyly of the Orchideae.

Nuclear ribosomal DNA of Orchidinae was first sequenced by Cozzolino *et al.* (1996); five species of *Orchis s.l.* were resolved using

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[1] Taxonomy largely follows the highly species-rich classification of Delforge, as modified by Bateman *et al.* (1997).

ITS1 into two of the three groups subsequently recognized by Pridgeon *et al.* (1997): '*O.*' *coriophora*, '*O.*' *morio* and '*O.*' *laxiflora* (our *Anacamptis s.l.*[1]) versus *O. simia* and *O. purpurea* (our *Orchis s.s.*). A greatly increased scale of molecular analysis in the Orchidinae was heralded by the ITS matrix of Pridgeon *et al.* (1997) and Bateman *et al.* (1997). The 88 sequences of the ITS1–5.8S–ITS2 assembly submitted provided the forerunner of the study of Bateman *et al.* (submitted), which in turn is the basis for this text. Data were analysed in detail, and subsequent discussion topics included sequence evolution, inter- and infrageneric relationships and hybridization frequencies, comparison with the results of past studies (both non-phylogenetic and phylogenetic), key synapomorphies, homoplastic characters (including floral morphology and pigmentation), and misleading information detected in the extensive literature on the group. Their primary taxonomic conclusion was that *Orchis* as then widely delimited was triphyletic. After discussing levels of sequence disparity necessary for particular taxonomic ranks and reviewing the taxonomic history of the genus, the authors reassigned the majority of species in the former *Orchis* to expanded concepts of *Neotinea* and especially of *Anacamptis*. Other taxonomic losses were the inclusions of *Nigritella* into an otherwise paraphyletic *Gymnadenia*, the monospecific *Aceras* into *Orchis s.s.*, and the monospecific *Coeloglossum* into *Dactylorhiza*.

Douzery *et al.* (1999) combined nine ITS sequences of Orchidinae and five of Habenariinae carried forward from the study of Pridgeon *et al.* (1997) with a further six Habenariinae and 30 Diseae, revealing a paraphyletic Diseae *s.l.* (Diseae *s.s.* sandwiched within a polyphyletic Coryciinae, with Satyriinae relatively derived) subtending a strongly monophyletic Orchidinae as sister to a monophyletic Habenariinae. However, except for the near-basal divergence of *Disa*, this study differed from the preceding *rbcL* phylogenies. Within the Orchidinae–Habenariinae, the tree showed little topological similarity to the preceding, more intensively sampled ITS analysis.

Luo and Pridgeon (in preparation) similarly used the ITS framework of Pridgeon *et al.* (1997) to examine in greater detail single additional sequences from eastern Asian representatives of the Habenariinae genera *Habenaria* and *Peristylus*, and the Orchidinae genera *Platanthera*, *Galearis*, *Gymnadenia*, *Neottianthe*, *Amitostigma*, and *Ponerorchis*, together with eight putative species of *Hemipilia*. Relationships among the eastern Asian clade, consisting of the four latter genera, resembled those observed in the later, more comprehensive study (Bateman *et al.*, submitted), but generic relationships within the ostensible sister group of *Platanthera–Gymnadenia–Dactylorhiza–Pseudorchis–Orchis s.s.–Galearis* again differ from the earlier ITS study of Pridgeon *et al.*

Most of the 88 ITS sequences analysed by Pridgeon *et al.* (1997; sample details given in their Table 2) were carried forward into the more detailed analysis of Bateman *et al.* (submitted), which provides the basis of the remainder of this section. Materials supplied by several collaborators, together arguably encompassing all genera of the more narrowly delimited genera of Orchidinae barring the monospecific *Steveniella*, encompass the majority of the widely recognized species (cf. Delforge 1995). Coverage of the newly expanded concept of Habenariinae remains undesirably sparse (cf. Dressler 1993).

Relationships within the major clades

The ITS phylogenies of Bateman *et al.* (submitted), plus as yet unpublished *trnL* phylogenies for a subset of the coded taxa (Bateman *et al.*, unpublished), delimited 11 well-supported clades of Orchidinae (Fig. C.5), each encompassing from one to four genera as recircumscribed by Bateman *et al.* (1997), whereas most of the perceived relationships among those major clades received weaker bootstrap support. Here we consider briefly each of those 11 clades in turn, beginning with the most derived, before returning to summarize higher level relationships and broader patterns.

Ophrys (28 coded taxa): Although still a meagre proportion of the 142 putative species listed by Delforge (1995), these 28 species encompass all of his informal groups and subgroups. The monophyly of the genus is strongly supported, but relationships within the genus are poorly resolved and interpretations therefore tentative. A heterogeneous and apparently paraphyletic group of species with relatively simple labella gave rise to a relatively derived and species-rich group with complex three-dimensional labella and beaked connectives. Notable features are the monophyly of the morphologically distinct *fusca*~*lutea*[2] group and the basal divergence of *Ophrys apifera* within the derived group that is rich in morphologically similar 'species'.

Serapias (seven coded taxa): Although well covered taxonomically, even less resolution is evident in *Serapias*. Like *Ophrys*, the monophyly of *Serapias* is strongly supported, reinforcing its unequivocal morphological cohesion.

Anacamptis (16 coded taxa): This fairly well-supported clade encompasses all species of the former *Orchis* that possess 36 (or, in the case of *A. papilionacea*, 32) chromosomes (Pridgeon *et al.* 1997). Molecular, morphological, and cytological (D'Emerico *et al.* 1996*b*) divergences are on average high within the clade (Fig. C.5). Monophyletic groups with both molecular and morphological cohesion include *morio*~*boryi*, *fragrans*~*sancta*, and *laxiflora*~*palustris*, though the more morphologically individualistic *A. pyramidalis*, *A. papilionacea*, and *A. collina* are, unsurprisingly, more ambiguously placed (*A. collina* also yielded strongly divergent allozyme patterns according to Rossi *et al.* 1994). The tentative suggestion of Bateman *et al.* (1997) that the *laxiflora*~*palustris* clade (represented in their tree only by *A. laxiflora*) could merit generic segregation received some support from the subsequent tree (Fig. C.5); *Anacamptis* as currently delimited lacks strong bootstrap percentages.

The five-step ITS disparity between *A. coriophora s.s.* and *A. fragrans* and the six-step disparity between *A. palustris s.s.* and *A. robusta* indicate that Bateman *et al.* (1997) were perhaps premature in treating *A. fragrans* and *A. robusta* as subspecies rather than species. Moreover, their inclusion of *A. morio* subsp. *picta* as a

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[2] Within the text of this section, the symbol '~' is used to indicate an inclusive clade bracketed by the two explicitly stated end-members (e.g. *Ophrys apifera*~*Ophrys scolopax* on Fig. C.5).

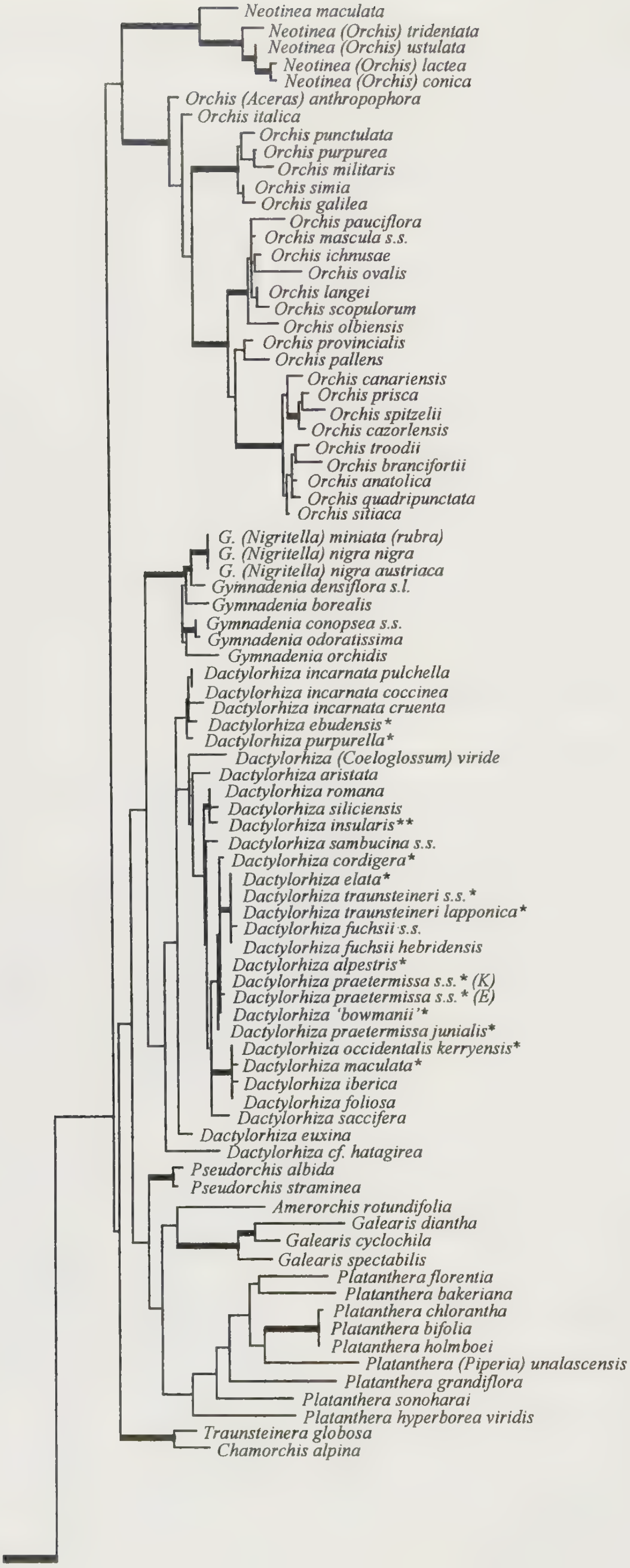

Figure C.5b

Fig. C.5 a, b. Recent provisional ITS phylogeny for 172 coded taxa of Orchidinae and selected Habenariinae (Bateman *et al.*, submitted). *Disa uniflora* was the sole outgroup, given the accepted monophyly of Orchideae, in a heuristic search using PAUP* (Swofford 1998) and including the least ambiguous indels as a gap matrix. For full analytical protocols see Bateman *et al.* (submitted), and for discussion of base composition and bias see Pridgeon *et al.* (1997). Thickened branches have >80% bootstrap support. The cladogram was randomly selected from about 30 000 most parsimonious trees of Fitch length of 2435 steps, consistency index of 0.36 (0.33 excluding autapomorphies) and retention index of 0.80. Fig C.5b is a continuation of Fig. C.5a. Within *Dactylorhiza*, a single asterisk indicates tetraploid species, and a double asterisk indicates triploid species.

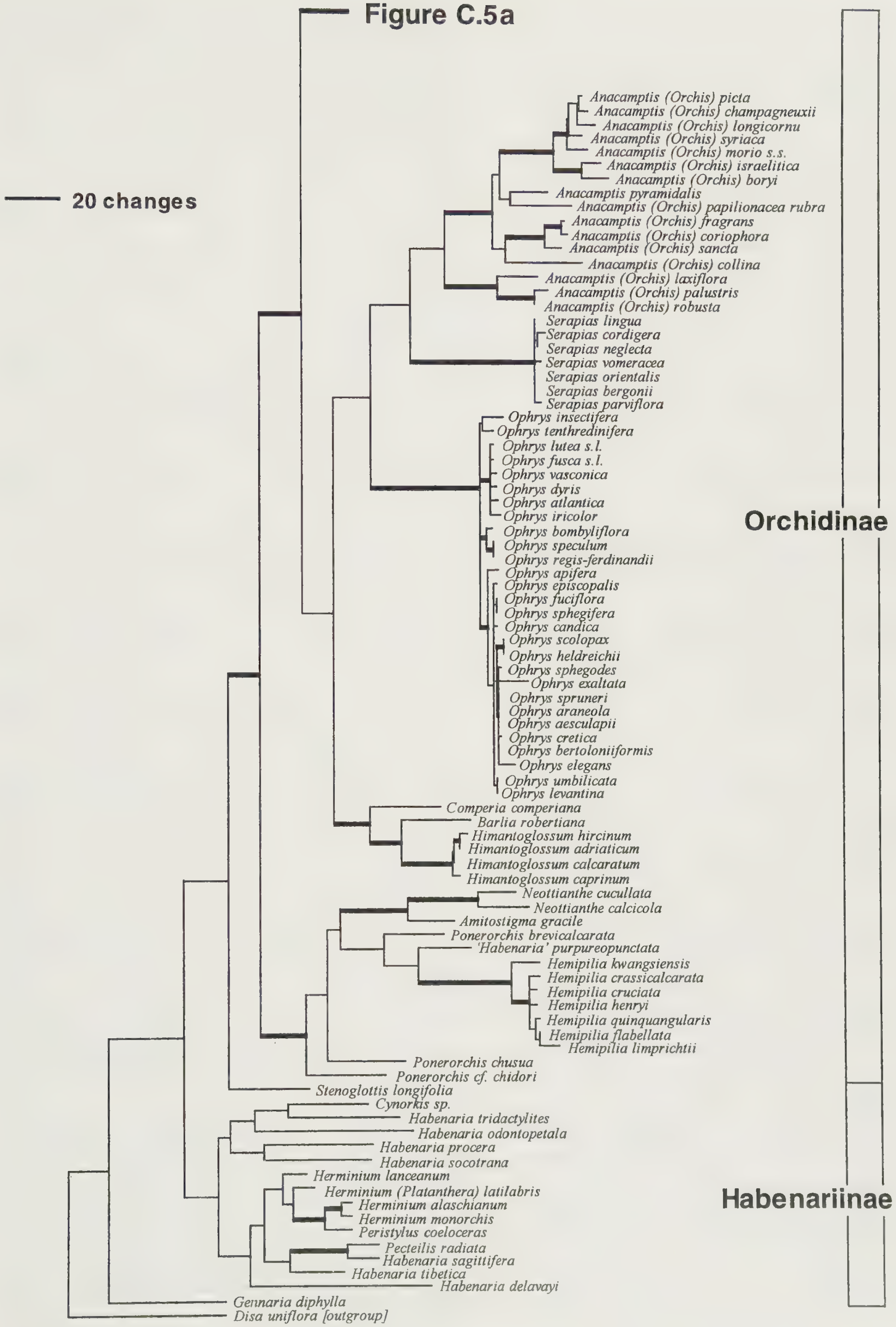

Fig. C.5a, b. *(continued)*

synonym of *A. morio s.s.* is not upheld; rather, *A. morio* subsp. *picta* is more closely related to *A. champagneuxii* and to the newly incorporated *A. longicornu* (Poir.) R. M. Bateman, Pridgeon & M. W. Chase.

Comperia–Barlia–Himantoglossum (six coded taxa): This is a well-resolved clade defined by large, elongate, trilobed labella. The morphologically distinct, arguably monospecific genera *Comperia* (a new addition to the ITS analysis) and subsequently *Barlia* are successive sister groups to the supposedly more species-rich but poorly resolved *Himantoglossum* clade. As expected, the questionably distinct *H. calcaratum* (G. Beck) Schltr. proved similar to the other eastern Mediterranean species in terms of ITS sequences. Recent sequence data (Pridgeon *et al.*, unpublished) indicate that *Steveniella* also falls into this clade.

Neotinea s.l. (five coded taxa): The formerly monospecific *Neotinea* was expanded by Pridgeon *et al.* (1997) and Bateman *et al.* (1997) to encompass the small number of small-flowered, essentially trilobed-lipped species of the *ustulata* group that were formerly included in *Orchis s.l.* These could in theory have been treated as a genus separate from the more narrowly delimited original concept of *Neotinea*, given the relatively long molecular branch and distinct vegetative markings of *N. maculata*, but there are clear similarities in floral morphology. As expected, *N. tridentata* ssp. *conica* (Willd.) R. M. Bateman, Pridgeon & M. W. Chase proved similar to *N. lactea*, though the four-step disparity indicates that Bateman *et al.* (1997) may have been in error to assign subspecific status to the former.

Traunsteinera–Chamorchis (two coded taxa): One of the more surprising outcomes of the expanded matrix of Bateman *et al.* (submitted) is the strongly upheld pairing of the two arguably monospecific alpine/boreal genera *Traunsteinera* and *Chamorchis*. *Traunsteinera* is tall with large leaves evenly spaced along the stem, bearing a compressed conical raceme of pale pink flowers with trilobed labella that resemble those of *Neotinea s.l.* In contrast, *Chamorchis* has a short stem that is subtended by basally concentrated filiform leaves and bears an elongate raceme of pale green flowers and entire, spurless labella; they are reminiscent of *Dactylorhiza* (formerly *Coeloglossum*) *viridis* or *Pseudorchis*. However, the two morphologically distinct genera are sufficiently similar in ITS sequences to be potentially viewed as congeneric.

Orchis s.s. (25 coded taxa): Sampling within true *Orchis* has been much improved since Pridgeon *et al.* (1997). Nonetheless, the basic structure originally observed within the clade is upheld; *Orchis* (formerly *Aceras*) *anthropophora* and *O. italica* are basally divergent and render the more primitive 'anthropomorphic' group paraphyletic. The remaining five anthropomorphic species, now including the dominantly yellow-flowered eastern Mediterranean species *O. punctulata* Steven ex Lindl. and *O. galilaea* (Bornm. & M. Schulze) Schltr., form a well-supported clade (*punctulata~militaris*), which is sister to the species-rich group of broad-lipped *Orchis* that are morphologically convergent (and formerly classified) with *Anacamptis longicornu~boryi*.

This clade in turn reveals a near trichotomy of the yellow-flowered *O. pallens* group, *O. mascula* and its segregates, and the *O. spitzelii–anatolica–quadripunctata* complex. This topology confirms the placement predicted by Bateman *et al.* (1997) for *O. spitzelii* and its relatives but shows less molecular divergence than might be expected from the considerable morphological diversity of this species group. The substantial allozymic divergence between *O. quadripunctata* and the morphologically similar *O. brancifortii* Biv. reported by Rossi *et al.* (1994) is reflected in the ITS tree. The most surprising result was the inclusion of the yellow-flowered *O. pauciflora* in the otherwise purple-flowered *O. mascula* group, incontrovertibly separated from *O. provincialis* and *O. pallens*. This placement was confirmed by sequencing a second specimen of *Orchis pauciflora* from a different country, refuting the Bateman *et al.* (1997) treatment of *pauciflora* as a subspecies of the morphologically similar *O. provincialis*.

Pseudorchis–Amerorchis–Galearis–Platanthera s.l. (15 coded taxa): This clade receives less bootstrap support than the preceding clades, with the geographically widespread *Pseudorchis* being the most tenuous (Fig. C.5). There is negligible ITS divergence between *Pseudorchis albida* and the recently segregated *Pseudorchis straminea* (Fernald) Sojak (Reinhammar 1995; Reinhammar and Hedrén 1998). The next group to diverge consists of the monospecific *Amerorchis*, which as anticipated by Pridgeon *et al.* (1997) is placed as sister to *Galearis*; they are sufficiently divergent to justify Hultén's (1968) generic segregation of *Amerorchis*.

Although sampling of *Platanthera s.l.* is sparse compared with the detailed ITS analysis of 36 species presented by Hapeman and Inoue (1997), new additions reveal some interesting relationships. As anticipated, the single analysed species of '*Piperia*' (representative of three species as described by Luer 1975 or four as listed by Dressler 1993) nests within (and thus should be synonymized with) *Platanthera*. The Chinese *Platanthera bakeriana* Kränzl. is sister to the Japanese *P. florentia*, and the previously noted negligible divergence between *P. bifolia* and *P. chlorantha* is extended to include the putative species *P. holmboei* H. Lindb. from montane regions of the eastern Mediterranean.

Dactylorhiza s.l. (29 coded taxa): Increased sampling of the *Dactylorhiza* clade (including the formerly monospecific genus *Coeloglossum*) retained the original pattern of relationships observed by Bateman *et al.* (1997) and Pridgeon *et al.* (1997), though the positions of the additional taxa provide further fascinating insights. Interpretation of the genus is complicated by extensive and iterative polyploidy (e.g. Averyanov 1990; Hedrén 1996; Bateman *et al.*, unpublished; asterisked taxa in Fig. C.5) and relatively low levels of ITS divergence.

Firstly, the south-east Asian *D. hatagirea* (D. Don) Soó is sister to the rest of the genus and sufficiently distinct to weaken the formerly strong bootstrap support for the monophyly of the genus (cf. Pridgeon *et al.* 1997); this species warrants more detailed study, as it may merit genus-level distinction. The addition of *D. euxina* (Nevski) S. K. Cherepan. below the relatively primitive diploids of the *D. incarnata* complex is no surprise, unlike the inclusion of the Scottish allotetraploids *D. purpurella* (T. Steph. & T. A. Steph.) Soó and *D. ebudensis* (Wief.) P. Delforge, which clustered with the *traunsteineri* complex on morphometric (McLeod 1995) and AFLP

(Hedrén, in preparation) evidence. Next to branch off successively are diploids such as *D.* (formerly *Coeloglossum*) *viridis*, *D. aristata*, and the *D. sambucina* (L.) Soó complex. *Dactylorhiza saccifera* does not group with the morphologically similar *D. fuchsii*. *Dactylorhiza occidentalis* (Pugsley) P. Delforge, now viewed as a probable autopolyploid, falls into the morphologically heterogeneous clade of the diploids *D. iberica* and *D. foliosa* and the autopolyploid *D. maculata*. Out of a plexus of the *D. majalis* aggregate of allopolyploids (*D. cordigera*~'*bowmanii*') emerges the diploid *D. fuchsii* complex, plus allopolyploids of the *D. traunsteineri* complex and *D. elata* from the western Mediterranean.

Credible interpretation of these intriguing patterns will require careful integration of ITS sequences with *trnL* sequences (Bateman *et al.*, unpublished), AFLPs (Hedrén, in preparation), allozymes (e.g. Hedrén 1996; Bateman *et al.*, unpublished) and morphometric ordinations (e.g. Bateman and Denholm 1989). For the present, and despite considerable research effort, *Dactylorhiza* remains perhaps the least understood of the predominantly European clades of Orchidinae.

Gymnadenia s.l. (eight coded taxa): As in *Dactylorhiza*, sampling in *Gymnadenia s.l.* has more than doubled since the publication of Pridgeon *et al.* (1997), who took the controversial step of sinking the morphologically distinct '*Nigritella*' back into synonymy with *Gymnadenia s.s.*, which would otherwise have been paraphyletic. The clade is presently the subject of several research projects using a range of techniques; all reinforce the then tentative decision of Bateman *et al.* (1997) to separate *G. densiflora* A. Dietr. and *G. borealis* (Druce) R. M. Bateman, Pridgeon & M. W. Chase from *G. conopsea* as full species on the basis of significant ITS divergence (albeit less than was originally inferred by Bateman *et al.*). Although tetraploid karyotypes have been reported in both *G. densiflora* (Mrkvicka 1993) and *G. conopsea s.s.* (K. Marhold, personal communication), *Gymnadenia s.s.* appears predominantly diploid in the UK (J. Bailey, personal communication) and elsewhere in Europe. In contrast, the more widely distributed species of '*Nigritella*' analysed by us are tetraploids (e.g. Teppner and Klein 1985*a*, 1998); we have yet to sequence the more localized diploids such as '*N.*' *corneliana* and '*N.*' *rhellicani* (Teppner and Klein 1985; D'Emerico, this volume).

On present evidence, the north-west European *G. borealis* and Asian *G. orchidis* Lindl. vie for the most basally divergent placement, the often sympatric *G. conopsea s.s.* and *G. odoratissima* are identical in their ITS sequences despite their clear morphological differences, and the most robust species *G. densiflora* is the somewhat surprising sister species to the diminutive '*Nigritella*' complex, species of which are undifferentiable on ITS evidence (Bateman *et al.*, submitted).

Ponerorchis–Hemipilia–Amitostigma–Neottianthe (14 coded taxa): No members of this archetypal Asian clade were sequenced by Pridgeon *et al.* (1997). The group has since been actively targeted for study. The results of Bateman *et al.* (submitted; Fig. C.5) can be compared with the strict consensus ITS tree of Luo and Pridgeon (in preparation). Both studies reveal a basal dichotomy separating '*Habenaria*' *purpureopunctata* K. Y. Lang and *Hemipilia s.s.* from the remainder of the clade. '*Habenaria*' is certainly not the correct generic assignment; indeed, given its high divergence, *H. purpureopunctata* appears to merit distinction as a new monospecific genus, provided that reliable morphological autapomorphies can be identified. Relationships within the well-sampled *Hemipilia s.s.* are poorly resolved, with the exception of *H. kwangsiensis* T. Tang & F. T. Wang ex K. Y. Lang.

As in the analysis of Luo and Pridgeon (in preparation), Bateman *et al.* (submitted) found *Ponerorchis* to be weakly paraphyletic, subtending a well-supported clade of *Amitostigma* plus *Neottianthe*. However, in Fig. C.5 the genus appears diphyletic. Further sampling and morphological study are prerequisites for eventual taxonomic revision of the genus. Overall, the genera currently recognized in this wholly Asian group survive the test of monophyly well, despite the long-term controversies that they have engendered (cf. Vermeulen 1972; Soó 1974; Chen 1982; Luo and Chen, in press; P. Cribb, personal communication).

'Habenariinae' (16 coded taxa): Once again, the available sample size has more than doubled over the past two years, though it remains a minor fraction of the *c.* 1040 species estimated to comprise the subtribe (including 110 species previously placed within the then more broadly delimited Orchidinae by Dressler 1993). Phylogenetic relationships within subtribe 'Habenariinae' are highly equivocal; both our past (Pridgeon *et al.* 1997) and present (Fig. C.5) analyses demonstrated varying degrees of paraphyly within the group, yet it was shown as monophyletic (including *Stenoglottis*) in the taxonomically broader ITS study of Douzery *et al.* (1999), implying that outgroup choice may profoundly affect perceptions of the validity of the group.

Current evidence indicates that the species-rich genus *Habenaria* will require profound fragmentation and reconstruction around monophyletic generic segregates (a parallel process to that experienced by the Orchidinae over the past century: Bateman *et al.* 1997). *Herminium* appears likely to survive as a monophyletic group, though incorporating some Asian species currently assigned to *Peristylus* and even to *Platanthera* (Fig. C.5). The position of monospecific *Gennaria* is unstable when taxon composition is altered and may merely reflect an artefact. The current placement of *Cynorkis* is also questionable. *Stenoglottis* especially merits further study, as it appears to define the most appropriate boundary between 'Habenariinae' and Orchidinae (see also Douzery *et al.* 1999).

Relationships among the major clades: correlating molecular and morphological evidence

Whereas most of the clades described in the previous section are viewed as well-supported, comparison of Figs C.5, C.6a, and C.6b demonstrates that the relationships *among* most of those clades are far more ambiguous. In the analysis of Bateman *et al.* (1997) and Pridgeon *et al.* (1997), exclusion (Fig. C.6a) and inclusion (Fig. C.6b) of insertion–deletion events (indels) generated contrasting topologies that agreed only in the well-supported monophyly of the re-circumscribed Orchidinae and in the only moderately supported relationships within the *Anacamptis~Himantoglossum* clade, which is delimited by a chromosomal reduction from $n = 21$ to $n = 18$ and a tendency toward viscidial fusion. In Fig. C.6a, the sister-groups to this clade are *Neotinea s.l.* and *Orchis s.s.–Traunsteinera* respectively, together generating a clade that is weakly supported by ITS but in theory is strongly supported by morphological characters such as globose tubers, sheathed inflorescences, and membranous bracts (Vermeulen 1947; Pridgeon *et al.* 1997).

Pridgeon *et al.* viewed this topology as more credible in overall patterns than that generated from nucleotides plus indels (Fig. C.6b), where *Orchis–Traunsteinera* was shown as sister to a fusiform/digitate-tubered clade, and *Neotinea s.l.* appears to be the sister of the rest of Orchidinae. However, the representation of the *Platanthera*, *Dactylorhiza*, and *Gymnadenia* groups was viewed as more credible in Fig. C.6b than in Fig. C.6a, with the fusiform-tubered *Platanthera* appealingly depicted as an intermediate form leading to the digitate tubers, chromosomal reduction ($n = 21 > 20$), and tendencies for both polyploidy and hybridization that unite *Dactylorhiza* with *Gymnadenia.* The polarity of these key characters is, of course, the converse in Fig. C.6a, in which these genera appear primitive rather than derived (a topology more consistent with biogeographic patterns: Bateman *et al.*, submitted).

This trio is also evident in the new expanded tree (Fig. C.5), with the ambiguously placed *Traunsteinera–Chamorchis* shown as sister (i.e. no longer linked to *Orchis s.s.* as was previously believed). This makes better morphological sense than Figs C.6a and C.6b, as *Orchis s.s.* possesses inflorescence sheaths and membranous bracts, whereas *Traunsteinera* and especially *Chamorchis* are more akin to *Platanthera* in these features. The Bateman *et al.* tree also recovers in its original topology the derived clade that possesses the cytological synapomorphy of $n = 18$. However, *Neotinea s.l.* is now depicted as sister to *Orchis s.s.* This again is a morphologically credible outcome previously advocated by, for example, Delforge (1995); also, D'Emerico (this volume) noted chromosomal similarities between the *Neotinea* group and the more primitive, 'anthropomorphic' species of *Orchis s.s.*

The pairing of *Neotinea* and *Orchis s.s.* is shown somewhat unintuitively as sister to *Traunsteinera–Platanthera–Dactylorhiza–Gymnadenia*, thereby once again refuting Vermeulen's (1947) concept of a clade united by globose root tubers (*sensu* Stern 1998), sheathed inflorescences, and membranous bracts; rather, these characters are optimized as plesiomorphic, and, once again, the crucial nodes on the 'spine' of the cladogram have only low to moderate bootstrap support.

The greatest novelty of the upgraded ITS tree is the inclusion of the Asian *Neottianthe~Hemipilia* clade and its clear position as sister to the remaining clades within the Orchidinae *s.s.* Given the great morphological and karyotypic diversity evident among 'Habenariinae', including this Asian Orchidinae clade in the overall analysis significantly improved the chances of obtaining realistic polarities for morphological and cytological characters (Luo and Chen, in press; Luo and Pridgeon, in preparation). The few relevant karyotypes of $2n = 42$ available for both *Amitostigma gracile* Schltr. (Tanaka 1965; D'Emerico, volume) and *Neottianthe cucullata* Schltr. (Sundermann 1980) argue against plesiomorphy for the $2n = 36$ clade. Inflorescences are unsheathed, bracts non-membranous, and tubers relatively small and globose. Interestingly, these are plesiomorphic features that also characterize northern hemisphere temperate 'Habenariinae' such as *Herminium.*

The above discussion focuses on 'mapping' across the ITS trees highly conserved non-molecular characters of low homoplasy and therefore of potentially high phylogenetic information content, notably karyotype and tuber morphology. However, characters incurring greater levels of homoplasy are more likely to play central

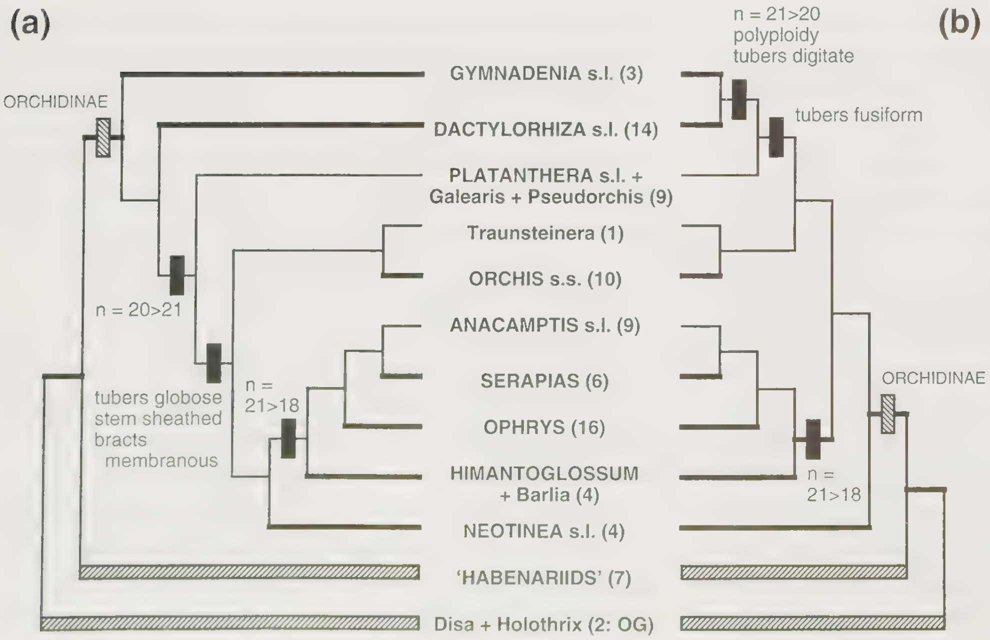

Fig. C.6. Summary of the ITS phylogenies of the Orchidinae presented by Pridgeon *et al.* (1997), as estimated without (a) and with (b) indels. Thick branches indicate >80% bootstrap support; cross-hatched branches indicate paraphyletic groups (see also Bateman *et al.* 1997, submitted). Parenthetic figures denote the number of named taxa analysed for each major clade.

roles in lower-level (and potentially co-adaptive) speciation events. Examples discussed in greater detail by Pridgeon *et al.* (1997) and Bateman *et al.* (1997, submitted) included floral pigmentation, discrete vegetative markings, expanded attractant bracts, labellar papillae, spur dimensions and posture, sepal–petal connivence to form a 'galea', degree of development of a bursicle, and the number of viscidia. Most of these characters have obvious implications for determining pollinator specificity (cf. Dafni 1987).

Lastly, the frequent records of hybrids in the Orchidinae require considerable critical appraisal when, as in the vast majority of cases, they are based entirely on morphological comparison. Infrageneric hybrids are often under-recorded due to preclusion of identification by morphological overlap between the putative parents. In contrast, past records of *inter*generic hybrids are probably vastly inflated due to recognition of phylogenetically spurious genera and erroneous identification of morphological extremes of single species, including teratological mutants (Bateman *et al.* 1997, submitted). The few credible records of bigeneric hybrids to survive our taxonomic revision of the Orchidinae are generally sister-genera. The most common hybrids between the 11 major clades discussed above also occur between sisters or near-sisters, such as *Gymnadenia* × *Dactylorhiza*, *Pseudorchis* × *Dactylorhiza*, and *Anacamptis s.l.* × *Serapias*. Hybrids between *Traunsteinera* and members of the fusiform–digitate-tubered clade support its revised ITS placement as their sister-group (Bateman *et al.*, submitted).

Taxonomic implications

Although the ITS cladogram of Pridgeon *et al.* (1997) and subsequent, monophyly-driven taxonomic rearrangements formalized by Bateman *et al.* (1997) caused predictable controversy, they have since begun to permeate the secondary literature. The generic transfers involved the incorporation of *Coeloglossum* into the conserved *Dactylorhiza*, *Nigritella* into *Gymnadenia*, *Aceras* into *Orchis s.s.*, and the expansion of the formerly monospecific *Neotinea* and *Anacamptis* to encompass tranches of the formerly triphyletic *Orchis s.l.* Further taxonomic requirements of the expanded tree (Fig. C.5) are the synonymization of *Piperia* into *Platanthera*, as well as the possibilities of: 1) more narrowly delimiting the apparently para- or polyphyletic *Ponerorchis*; 2) establishing a new monospecific genus as sister to *Hemipilia*; 3) erecting *Dactylorhiza hatagirea* as a new sister-genus to the other more derived dactylorchids; and 4) redelimiting the *Anacamptis laxiflora*~*robusta* clade as a new genus. Even if all these transfers were implemented they would affect only an estimated 11% of the total number of species widely recognized within Orchidinae *s.s.* (Bateman *et al.* 1998).

There are also clear implications for potential hierarchical classifications *within* the more species-rich genera. Bateman *et al.* (1997) and Pridgeon *et al.* (1997) discussed at length the severe taxonomic problems that had developed when over two centuries of taxonomic research attempted to shoehorn the triphyletic *Orchis s.l.* into various infrageneric classifications. Indeed, new results presented by Bateman *et al.* (submitted) require further dismantling of Vermeulen's (1972, 1977) classification of *Orchis s.l.*, because his subsections *Punctulatae*, *Provincialae*, and *Masculacae* (see Bateman *et al.* 1997) have all proven to be non-monophyletic. Phylogenetically based infraspecific classification is now feasible for *Orchis s.s.*, *Anacamptis s.l.*, and the well-studied *Platanthera*–'*Piperia*' (Hapeman and Inoue 1997). However, a realistic treatment of *Dactylorhiza* will require additional studies to accommodate fully the consequences of iterative polyploidy, and those of *Ophrys* and *Serapias* will require more effective molecular (and morphometric) tools for delimiting *bona fide* species and determining their relationships, given the undoubted recency of their respective radiations.

It is also tempting to generate classifications that group the 11 well-founded clades discussed individually above, though some poor bootstrap percentages along the 'spine' of the cladogram indicate that further formal classification would be premature and that a simultaneous analysis of multiple data sources (e.g. adding morphological and plastid sequence data: Bateman 1999) is required. The taxonomic history of Orchidinae was well reviewed by Klinge (1898), Vermeulen (1947), and Bateman *et al.* (1997), yet there remains an opportunity to compare in greater detail the supra-generic classifications of such orchidological luminaries as (in chronological order) Linnaeus, Haller, Swartz, Brown, Richard, Lindley, H. G. L. Reichenbach, H. G. Reichenbach, Klinge, Schlechter, Camus, Vermeulen, Dressler, and Delforge. All unknowingly deviated from the dictates of monophyly due to typological reliance on a relatively small number of often highly homoplastic morphological characters.

For example, Dressler (1993) classified Orchidinae primarily according to tuber morphology into four tentative 'alliances' (tabulated with distributional data as Table 1 of Pridgeon *et al.* 1997). Of these, alliance 4, consisting of the African genera *Holothrix* and *Bartholina*, certainly does not belong in Orchidinae, nor is its ITS placement in 'Habenariinae' by Douzery *et al.* (1999) convincing as it is subtended by a long branch. We believe that the group may even lie outside the Orchideae. Figure C.5 demonstrates that Dressler's alliance 1, incorporating genera with minimal tuber development such as *Galearis* and *Amerorchis*, is a subgroup of the fusiform-tubered *Platanthera* clade, which occurs in Dressler's alliance 2 alongside digitate-tubered genera of the *Dactylorhiza* and *Gymnadenia* clades. Also erroneously placed in alliance 2 are the far more primitive Asian Orchidinae '*Chusua*' (=*Ponerorchis*) and the dominantly African 'Habenariinae' *Brachycorythis* (Douzery *et al.* 1999). The globose-tubered alliance 3 is the most genus-rich and morphologically heterogeneous assembly, mixing primitive Asian genera such as *Amitostigma* and *Hemipilia* with the derived $2n = 36$ clade of *Himantoglossum*~*Anacamptis* and the globose-tubered sister-groups (*Neotinea s.l.*–*Orchis s.s.* and *Traunsteinera*–*Chamorchis*) of the fusiform–digitate tubered clade. Also included is the as yet unsequenced South African genus *Schizochilus*.

Thus, Dressler's (1993) classification contains valuable insights into Orchidinae phylogeny but requires considerable modification in the light of the ITS phylogeny. No doubt the ITS pattern in Fig. C.5 will similarly require modifications as further data accumulate.

Remaining priorities for ITS sequencing within the Orchidinae include five supposed monospecific genera: the Eurasian *Steveniella* and Asian *Aceratorchis*, *Chondradenia*, *Symphyosepalum*, and *Pseudodiphryllum* (e.g. Vermeulen 1972; Dressler 1993). The need for further species-level sampling within genera already sequenced also focuses on (Eur)asia, where taxa such as '*Pseudorchis*' *frivaldii* (Hampe ex Griseb.) P. F. Hunt and *Gymnadenia camtschatica* Miyabe & Kudo represent potential basally divergent lineages of dominantly European clades, and where resolution is required of ambiguities in the *Neottianthe*~*Hemipilia* clade such as the apparent para- or polyphyly of *Ponerorchis* as currently delimited. Also, sequencing diploid species of '*Nigritella*' might aid understanding of the polyploids already sequenced by us. Further molecular phylogenetic research is especially desirable on putatively related tropical and southern African orchids. Bateman *et al.* (submitted) doubted that any belong in the Orchidinae *s.s. Brachycorythis* has already been shown to be a member of 'Habenariinae' (Douzery *et al.* 1999), and we suspect that *Schizochilus* and *Neobolusia* will follow suit. Moreover, *Holothrix* and *Bartholina* may even lie outside 'Habenariinae'. Certainly, 'Habenariinae' require far more intensive sampling for both sequencing and karyotypic studies. **(RB, PH, JP, LY, AP, MC)**

Pollination

Members of Orchideae display a wide variety of pollination systems and highly diverse floral traits. Our knowledge of their pollination biology varies considerably. Recently, an exhaustive collection of pollinator information for the European orchids was compiled by van der Cingel (1995), making the European members of Orchideae one of the best-studied groups. Nevertheless, pollinator information is still missing for a number of important European taxa and a significant number of non-European taxa. Pollinator information for Orchideae, as available, is provided as separate generic entries below. Literature references already compiled by van der Cingel (1995) are not repeated in detail, but a brief summary of the current pollinator knowledge is given.

Even if little information is available on the pollination of genera in the former Habenariinae, floral features and the few existing literature data indicate that the sphingophilous and phalaenophilous syndromes predominate in this group (Dressler 1981). In many species 'eye-pollination' (i.e. the attachment of pollinaria to the pollinators' eyes) seems the most frequent specialization. This is likely a consequence of the fact that moths and mosquitos do not possess many surfaces on which viscidia may adhere efficiently. All investigated 'Habenariinae' are scent-emitting, nectar-producing plants. Nectar is secreted in the spur where it accumulates in the tip.

Although the moth genus *Xanthorhoe* has been reported as a pollinator (Thien and Utech 1970), female mosquitos of the genus *Aedes* seem to be the main pollinators of *Habenaria obtusata* Richards (Thien 1969). When a mosquito takes nectar from the spur, one of its eyes is forced against the viscid pad of a pollinarium. The pollinarium adheres to the insect's eye when the proboscis is withdrawn from the spur. When a pollinaria-carrying mosquito visits another flower and places the proboscis in the slot leading to the entrance of the spur, it places the pollinia on the stigma located above the spur entrance. The flower has the throat entrance blocked by a flap, thus leaving two side passages; one such passage is probed each time so that the insect strikes either a viscidium or a stigma. Only some massulae rather than the entire pollinarium are usually removed from the insect and adhere to the stigma; therefore a single pollinarium can pollinate various flowers.

In a similar manner, the moth *Remigiodes remigina*, pollen vector for *Habenaria decaryana* H. Perrier, is stimulated to force the entire length of its proboscis into the spur, because the spur is longer than the proboscis, and the nectar is located at the distal end. As a consequence, the ventral inner surface of the moth's eyes presses against the viscidia, and the pollinarium is firmly attached. Afterwards, hygroscopic movement causes the rotation of the pollinaria into a position in which they can strike the stigma lobes in the flowers subsequently visited by the moth (Nilsson and Jonsson 1985).

The relationship between spur length and insect proboscis length is of great importance for effective pollination. Plants with a spur shorter than the proboscis of the insect have low fitness due to nectar loss and reduced pollination. The sphingophilous species not only possess a deeper spur as compared to the phalaenophilous species but have also developed long and upturned petal lobes, which form a physical guide for hovering moths and prevent unsuccessful side approaches to the flower.

In *Cynorkis uniflora*, a species without petal lobes, the pollinaria have extraordinarily long caudicles (approx. 16 mm) and are carried attached to the eyes of the hawk-moth genera *Nephele* and *Hippotion*. These two moths have medium tongue-lengths and fly in the early evening hours. They are attracted by the fragrance and rather light coloration of the *Cynorkis* flowers (Nilsson *et al.* 1992). The long and rigid hemipollinaria, which protrude from the pollinator's head, prevent access to the nectar if the insects attempt a side approach. When a pollinaria-carrying hawk-moth hovers in front of a flower, the pollen masses are caught by the pre-spur funnel in the centre of the flower and are mechanically guided by the raised rims of the basal portion of the labellum to strike the elongate stigmas.

Long pollinaria are also found in the southern African orchid *Bonatea speciosa*. Pollinaria are carried on the eyes of the hawk-moth *Theretra*. In this orchid species, however, the moths place their heads against the outer part of the rostellum lobes, and each pollinarium is carried independently. In fact, as a consequence of the presence of a tooth-like process at the mouth of the spur, moths are forced to enter the flowers from either side. Consequently, the insect will contact only one rostellum arm at a time and remove a single pollinarium during each visit (Johnson and Liltved 1997). This represents an interesting exception to the pollen single-packaging strategy of the majority of orchids, in which both pollinaria are removed simultaneously.

A notable exception to the eye-pollination syndrome is represented by *Herminium monorchis* R.Br. Flowers of this small plant with a short spur are subcampanulate and borne in a dense raceme. This species is pollinated by small wasps (mainly genus *Tetrastichus*), which are attracted by the floral fragrance. The insects enter the flower and insert their heads and forelegs into the short spur; in this way, the viscidia adhere to the outer surface of their femurs (Nilsson 1979, 1981). The close relationship with *Habenaria*, the presence of a spur nectary, and floral morphology indicate that *H. monorchis* may have evolved from a long-spurred ancestor adapted to anthophilous pollen vectors and eye-pollination syndrome. The recent discovery of *Habenaria montevidensis* (Singer and Cocucci 1997), a species with small, moth- or mosquito-pollinated flowers from which pollinaria are not attached to the eyes, demonstrates that alternative pollination strategies may have evolved more than once in this group.

Luo and Chen (1999) studied the pollination of *Hemipilia flabellata* Bur. & Franch. in north-west Yunnan, China. The orchid is pollinated by the bee, *Anthophora mangkamensis* (Apoidea). Because visits to the orchid are infrequent, they suggested that the orchid mimics the sympatric *Ajuga forrestii* Diels (Lamiaceae), which is frequently visited by the bee to collect nectar.

To the best of our knowledge, no detailed information on pollination biology has been reported in the literature for genera *Aceratorchis*, *Amerorchis*, *Amitostigma*, *Chondradenia*, *Comperia*, *Galearis*, *Neottianthe*, *Pseudodiphryllum*, and *Symphyosepalum*. The lack of pollinator information for these genera, as well as for many species in other genera discussed above, highlights the profound lack of knowledge of the basic biology of a large number of Orchideae. More details on the pollination biology of these plants are sorely needed for our understanding of orchid evolution and for the efficient conservation of these orchids and their fascinating interactions with their pollinators. **(SC, AW, AD)**

Cultivation

Orchideae are mostly terrestrial in habit, with a number of epiphytes and lithophytes. Their geographical distribution is wide, and their habitats extremely diverse. They range from arctic tundra and alpine regions to temperate and tropical forests and grassland, and from bogs to semi-desert areas. They can be said to encompass almost the entire gamut of soil types and root-zone conditions, and they often appear as pioneer plants following habitat disturbance. There are also many records of their thriving on polluted industrial sites where initially few other plants can establish. Despite this evidence of a robust and adaptable constitution, for many years the majority of genera in Orchideae have been considered difficult to grow. They have also for the most part been almost unobtainable in the orchid trade, with the exception of a small number of more horticulturally amenable genera (e.g. *Dactylorhiza*, *Habenaria*, and *Stenoglottis*). However, many genera have long featured in the collections of alpine and woodland plant enthusiasts, and in the Far East a number are grown by amateur enthusiasts in Japan.

In recent years there have been important advances in our understanding of the cultivation of terrestrial orchids, and particularly in their propagation from seed, using both aseptic techniques and mycorrhizal fungi. These advances in propagation techniques have made species and new hybrids more readily available and rekindled interest in the cultivation of a fascinating and diverse group.

For many of the genera under consideration, there is at best a patchy history of cultivation, often as part of botanic garden or research collections. However, the cultivation regimes and techniques recommended should prove successful in most instances, and are based upon accepted standard practices. For the best chance of success with little-known genera and species, it is particularly important that growers take note of the habitat factors relating to each species and adjust their methods accordingly.

The underlying cultivation principles for the mainly terrestrial orchids in Orchideae are broadly similar to those of orchids in general, including the more commonly grown epiphytes. These shared requirements also apply whether species originate from tropical or temperate regions. Many terrestrial orchids are adapted to succeed in low-nutrient regimes or to survive periodic drought, and these adaptations provide the key to their requirements in cultivation.

Most of the genera dealt with here have a definite dormancy period, when they have no parts above ground and perennate as tubers. Managing the dormant season requirements of the plants is a critical factor, particularly when grown in containers. Despite their ‘quasi-bulbous’ nature, they are not as resilient in their dormant state as many bulbous subjects.

Growing methods

Until comparatively recently terrestrial orchids were considered difficult to grow, or if success was achieved, were relatively short-lived in cultivation. However, there is now a track record of successful long-term cultivation of terrestrials world-wide, achieved by growers who have sought to understand the habitat requirements of terrestrials, particularly the plants’ relationships with their mycorrhizal fungi. Many genera benefit from what may be termed ‘organic’ or ‘ecological’ cultivation techniques designed to maintain and encourage mycorrhizal fungi, although a number of robust subjects will thrive under standard cultivation regimes.

Mature terrestrial orchid plants may retain a close relationship with their mycorrhizal fungi. Many possess much smaller root systems than other plants and benefit from the ability of the fungal symbiont to forage for nutrients over a larger volume of substrate or growing medium than that occupied by their own roots. For the genera dealt with here, we recommend a range of broadly standard cultivation techniques, which may be modified to take into account provenance and habitat. Providing the best conditions for many genera and species in the Orchideae may require protected cultivation in a greenhouse, shade structure or frame.

Major habitat factors

The most important habitat factors are:

provenance: providing information about seasonal temperature variations, rainfall patterns, and dormancy;

aspect: whether open, semi- or fully shaded; and *substrate*: whether acid or alkaline, high or low in organic matter, well-drained, moisture-retentive or with impeded drainage.

Provenance provides the most important initial clues to the grower; for example, terrestrial orchids from mediterranean climates with hot dry summers and mild moist winters tend to be winter growers. Plants from high latitudes or high elevations typically endure more severe winter conditions and are winter-dormant.

Aspect is of importance for many species, although those from open habitats often thrive under conditions with more shade than they experience in the wild, as typically occurs under protected cultivation. Shade-loving species from woodland habitats, however, may do poorly if grown under excessively high light conditions.

The basic substrate requirements for most orchids are similar. They require an open, well-drained and aerated growing medium, and are intolerant of stagnant conditions around their roots. These 'standard' conditions will also suit most of the species associated with wet or boggy conditions (with adjustments to their watering regime), although a few are effectively semi-aquatic and may require specialized conditions. Among the orchids that occur naturally in 'boggy' conditions, but which thrive under standard cultivation regimes, is the horticulturally important genus *Dactylorhiza*.

The nutrient status of orchid substrates is important, as the soils in which they occur naturally are often poor in nutrients. Intolerance of high-nutrient regimes in cultivation is common to most orchids and appears to be particularly true of terrestrials. Research also indicates that high nutrient regimes can disrupt the relationship between terrestrial orchids and their fungal symbionts.

Growing regimes

Species in Orchideae can be grown in various ways. A number of robust terrestrial species grow well as garden plants, either in beds and borders or when naturalized. However, protection from extremes of temperature and rainfall benefits most orchids in growth and quality of both plants and flowers. Given the cost and rarity in cultivation of many species, most growers opt for cultivation in containers in a greenhouse or other protected situation.

Orchids in the garden

Although many orchids will grow well in the open garden, in most cases they are not likely to succeed if in competition with other vigorous garden plants. Most of the genera dealt with here increase comparatively slowly by vegetative means. There are exceptions to this rule, such as the more robust *Dactylorhiza* species and *Serapias*. If conditions are favourable, some species will seed and become naturalized (see Naturalized orchids below).

Shady borders

Dappled shade is ideal for woodland species. Where this cannot be obtained from trees, a shaded border by a wall will often suffice. If none exists, a shade structure may be built over a bed covered with shadecloth or netting giving 50% shade, or laths 13 mm wide with a 13 mm gap (again resulting in 50% shade). Cloth has the advantage that it may be removed easily when natural light is not excessive, from autumn until spring.

Woodland garden soil is required in these situations and should be both open and moisture-retentive. Adding well-structured organic matter improves both aeration and moisture retention. For this purpose leaf mould, composted bark, and peat are ideal. Growing in raised beds with walls of stone, brick or wood gives greater control over soil conditions, improved drainage, and raises plants to where they may be appreciated more easily. An ideal soil mix for the woodland garden comprises a ratio of 2:2:1 organic matter (leaf mould, peat, composted bark, etc.), good open soil (loam if available), and sharp grit or coarse sand. The soil should be neutral to acid in pH, and the sand or grit lime-free, as most woodland plants grow in acidic conditions. To this mix a base-dressing of hoof-and-horn fertilizer at 10 ml per 10 litres should be added, renewed each year when top-dressing with fresh organic matter. Irrigation with soft water, maintaining a moist but not sodden soil helps to provide the humid microclimate that woodland plants require.

Marginal and bog gardens

Many orchids from marginal areas and bogs grow in high-light conditions, often in full sun, with continual moisture around the roots of the plants. In the wild, orchids in bogs tend to root shallowly in the well-aerated upper layers, in humus mats or in mosses such as *Sphagnum*. In gardens care should be taken to ensure that anaerobic or sour conditions do not arise, which may kill or damage the sensitive root systems of orchids. This is best achieved by ensuring that moving water passes through the marginal or bog area, avoiding potentially stagnant still conditions.

Orchids in open situations

A number of robust species can be grown in beds and borders, with modification of the soil to suit their requirements. More demanding species may be given discreet pockets of compost in a rock garden or raised bed or in troughs, sinks, and other large containers that remain outdoors all year round.

Warm sunny borders immediately next to a house or greenhouse wall afford protection for tender species and ideal conditions for those that require bright, dry situations. The latter may also thrive in scree beds (gritty, well-drained areas), given a sunny aspect. Alkaline or chalky soils can provide good conditions for a number of choice species. When growing in the open ground, effective drainage must be provided. The structure of heavy soils can be improved with sand or grit and organic matter. Sandy soils may be enriched and made more retentive by adding loam or organic matter. If planting in discreet pockets, as in a rock garden, the basic terrestrial compost mix may be used (see below) to provide soil entirely suited to the orchids.

Naturalized orchids

Given the right conditions, it is possible to create naturalized, self-perpetuating populations of genera including *Orchis* and *Dactylorhiza*. The best candidates for this treatment are species that occur locally in grassland, hedgebanks, road verges, and other such habitats. If a small population already exists within a garden the management of the area can be modified to encourage them to spread and colonize. Otherwise, given that the soil and aspect of the site are correct, plants may be introduced, although care must be taken to choose a species that will thrive and reproduce readily.

As with growing in beds and borders, naturalized orchids must not be out-competed by surrounding vegetation. Most of the best species for naturalizing grow in meadows or other grassland. They must be allowed to complete their growth cycle and shed their seed, after which the sward may be cut and removed (mimicking the natural cycle of hay meadows). The cultivation regime is geared toward retaining a mixed, open sward, which orchids can colonize. Fertilizers should not be used, as they may disrupt the orchid's mycorrhiza and will encourage rank growth of other herbage, which can overwhelm the orchids. Herbicide use should also be avoided; any rank-growing weeds should be removed manually. Pernicious perennial weeds should be cleared from the site before orchids are introduced; at this stage translocated herbicides may be applied to the foliage of the weeds as spot treatment, ideally by hand with a sponge or brush. Orchid species that succeed under this treatment include *Anacamptis morio*, *Orchis mascula*, and *Dactylorhiza fuchsii*.

Protected cultivation

Depending upon the degree of protection required, frames, greenhouses, or shade structures may be used. These can provide conditions ranging from complete climatic control to simple protection from the extremes of temperature and rainfall.

Frame cultivation

The standard bulb frame (effectively a bed either raised or at ground level with a glass or polycarbonate cover) suits many terrestrial orchids, especially those with summer dormancies. It provides dry conditions for dormancy and protection from the extremes of winter wet and cold. In spring and summer the frame should be open during dry weather for maximum ventilation and control of excessive temperatures, and closed as required to protect the plants from excessive or unseasonal rainfall. Plants may be grown in pots plunged in sand or grit or else planted directly into compost. To avoid the danger of dormant orchid tubers becoming desiccated in hot conditions occasional light waterings should be given to maintain a reserve of moisture in the compost. Frames also provide good conditions for shade-loving species, given the right aspect and extra shade as required.

Greenhouse cultivation

Greenhouse cultivation allows growers the greatest control over conditions. With the correct design and equipment, they can provide everything from the cool conditions required by frost-hardy species to the steamy heat of the tropical forest floor. For the majority of temperate terrestrials, the classical alpine house is ideal, with full ridge and side ventilation creating conditions in both winter and summer to suit many orchids in containers. A collection of both winter- and summer-growing temperate species can be successfully housed in such a structure.

The temperature to be provided will depend upon the provenance of the plants grown and will call for a combination of heating and ventilation, which may be automated. The atmosphere in greenhouses becomes dry in hot weather or when heating is provided. Relative humidity within the house can be increased by regularly wetting the floors or by installing a mist system beneath the benches, controlled by a timer switch or humidistat and solenoid valve.

Shade structures

Shade structures provide ideal conditions for woodland species. In areas with high light intensity and temperatures, many plants from open habitats will also grow better if provided with protection from such extremes. Wooden or metal structures should be covered with shadecloth or 13 mm slats at 13 mm spacing to provide 50% shade. In dry climates misting systems can be incorporated to provide increased humidity.

Growing in containers

Most orchids are grown in containers to achieve the greatest control of growing conditions over the year. Orchids can be grown in many different types of container, including clay and plastic pots. Clay pots are heavier, more stable, and dry more rapidly. Plastic pots are lighter and easier to manage but retain moisture longer. Orchids will grow equally well in either, as long as the grower adjusts the watering regime accordingly. This basic rule applies to the many different traditional and novel containers pressed into service for orchids. Many alpine-plant growers create miniature landscapes or mini-habitats in troughs and sink gardens. Such conditions again suit orchids well, given the correct soil type and non-competitive neighbours.

Growing bog orchids in containers

Growers who wish to grow bog orchids in semi-natural conditions can use the method described by Beckner (1979), which suits many species. This method seeks to create 'mini-bogs' with living *Sphagnum* moss, mimicking the plants' natural habitats. Plastic containers without drainage holes are used, preferably large and no less than 200 mm deep. A zone of permanently saturated medium to within 75 mm of the top is created. A few short narrow slits in the side of the container at that level are provided to allow for drainage of excess water. An additional 50 mm of planting medium is then placed above this, and the top 25 mm is finished off with living *Sphagnum* moss. The containers are set out in the open and receive full sun for most of the day. They must not be allowed to freeze solid.

The growing medium is 5:3:2 perlite:vermiculite:sphagnum moss peat. When planting, cover the orchid roots with living *Sphagnum* moss. Planting height may be varied to suit the habitat preference of the plants in question. Those that grow in wetter conditions should be close to the permanently saturated area, whereas those that grow under more marginal conditions may be planted higher. Rain or soft water only should be used. Fertilizers are not required and may indeed be harmful to the growth of *Sphagnum*. Once the *Sphagnum* is established and growing well, the health of the orchids is assured.

Growing in pots

Terrestrial orchids require larger pots than the size of the plant and its root system might suggest. The larger volume of compost dries out more slowly and thus offers more stable conditions for any mycorrhizal fungi present. The minimum pot size for mature terrestrial orchid plants, whether plastic or clay, should be 100 mm. Particularly for larger species, and when growing more than one plant in a pot, a container of 125–150 mm and upwards should be chosen. 'Squat' pots or half pots should be used; they have a greater surface area in relation to the volume of compost, which aids aeration and drying. Most terrestrial orchids should be repotted every year.

If clay or other more porous pots are preferred, a larger size is required than with plastic pots. They need to be checked for watering more frequently but have the benefit of a greater margin of error for those who may water too enthusiastically. Plastic containers may require extra holes to be cut or drilled into the base to ensure good drainage.

Composts

The soils in which members of Orchideae grow in the wild are extremely varied, including coarse leaf litter, heavy clay, chalk, and sand. Their requirements in cultivation can be met by a small number of basic composts, modified accordingly. A small number of the most robust species in genera such as *Dactylorhiza* can be grown in standard peat-based commercial composts. These are very much the minority. The orchid composts given here are designed to provide conditions to suit the fungal symbiont as well as the orchid.

Rather than give a great number of slightly different mixes, the basic composts here can be amended to suit each species. A number of tropical to subtropical genera (for example *Stenoglottis* species) may occur as epiphytes or in coarse leaf and twig litter and will grow well in fine- or medium-grade epiphytic orchid composts based on bark, perlite, and charcoal. They will also succeed in a coarse terrestrial compost, as given below.

COMPOST A: MEDIUM-FINE EPIPHYTE MIX

6 parts medium or fine grade orchid bark
3 parts chopped sphagnum moss (or fibrous sphagnum moss peat or similar)
1 part 'supercoarse' perlite
1 part medium grade charcoal
2 parts mixed beech/oak leaf mould (or similar) passed through a 13 mm sieve
Base-dressing of hoof-and-horn meal at 10 ml per 10 litres of mix

COMPOST B: COARSE TERRESTRIAL MIX

6 parts open-structured soil (fibrous loam if available), heat-sterilized
3 parts chopped sphagnum moss (or fibrous sphagnum moss peat)
3 parts 'supercoarse' perlite or coarse crushed grit (6 mm size)
1 part medium-grade charcoal
2 parts leaf mould (beech/oak or similar), passed through a 13 mm sieve
Base-dressing of hoof-and-horn meal at 10 ml per 10 litres

COMPOST C: STANDARD TERRESTRIAL MIX

This compost suits a wide range of terrestrials.

3 parts open-structured soil (fibrous loam if available), heat-sterilized
3 parts coarse gritty sand or crushed grit (6 mm size)
2 parts beech/oak leaf mould (or similar), passed through a 13 mm sieve
1 part composted pine bark (6 mm size)
Base-dressing of hoof-and-horn meal at 10 ml per 10 litres
*For species from alkaline habitats incorporate a further base dressing of dolomite limestone at 20 ml per 10 litre of mix

COMPOST D: WOODLAND TERRESTRIAL MIX

For woodland genera and those species that grow in moist or boggy habitats.

2 parts open-structured soil (fibrous loam if available), heat-sterilized
2 parts beech/oak leaf mould (or similar), passed through a 13 mm sieve
1 part fibrous sphagnum moss peat
1 part sharp sand or crushed grit (6 mm size)
Base-dressing of hoof-and-horn meal at 10 ml per 10 litres

COMPOST E: SOUTHERN AFRICAN TERRESTRIAL MIX

This compost is similar to that used by Australian growers. It may suit species from the Cape and possibly others from seasonally dry habitats.

2 parts coarse gritty sand
1 part heat-sterilized loam
1 part 'buzzer chips' (untreated hardwood or softwood chippings from sawmills) or bark chippings (6 mm size)
Base-dressing of blood and bonemeal at 10 ml per 10 litres of mix

Potting

Most orchids should be repotted while dormant, and most tuberous species should be repotted annually. Colony-forming species of genera such as *Serapias* may spend two to three years in the same container, but problems will arise if the compost structure deteriorates. The need to maintain good soil structure in containers and replenish the organic matter on a regular basis strongly indicates repotting yearly.

Most tuberous orchids have annual root systems that emerge from immediately below the dormant bud. They must be planted sufficiently deep to ensure that the roots are well covered with compost. Fill the pot with compost to 50 mm below the rim. Place the tubers in this layer, with the top of the dormant bud level with the compost, at ±37 mm below the final surface of the compost. Fill the pot to within 13 mm of the surface, and lightly water to settle the compost in the container. The watering regime thereafter is as required for the time of year and stage of growth of the plants.

Watering

The daily and seasonal watering of a mixed collection of terrestrial orchids varies according to their provenance and season when they are in growth. As with composts there are basic rules that apply to most plants.

WATER: QUALITY AND FREQUENCY

Water of a neutral to slightly acidic pH (6.5–7.0) is best. Rainwater is almost perfect, although slightly alkaline water (to pH 7.5–7.8) should present no problems. Terrestrial orchids appreciate a relatively even moisture regime while in growth, although they may require a more definite wet/dry cycle seasonally. They divide into two main groups: those from seasonally dry climates, which need to be dried-off for their dormancy, and those from high elevations and latitudes with a cold moist dormancy, which must be kept wetter. Evergreen species require water throughout the year and more when in active growth.

DRY SEASON DORMANT TERRESTRIALS

These should be lightly watered immediately after repotting to settle the compost and provide moisture for the new roots. As vegetative growth appears, water more frequently to keep them moist but not wet. Toward the end of the growing season, after the flowers have faded and as the rosettes begin to die off, reduce watering until it almost ceases. Containers must be checked every 3–4 weeks during hot weather and watered lightly if required to maintain some background moisture and keep the tubers plump.

COLD-SEASON DORMANT TERRESTRIALS

These require more moist conditions during dormancy and should be kept evenly moist when in growth.

Feeding and fertilizers

Most orchids are adapted to grow in poor soils. In cultivation this may manifest itself as an intolerance of generous feeding regimes and mineral fertilizers. Most tuberous terrestrials, if repotted regularly, do not require additional feeding. Those that are fed regularly when watered may suffer from the build-up of salts in the compost. To prevent this, feed at every second or third watering; the intermediate waterings will wash salts out of the compost. Orchids grown with the benefit of mycorrhizal symbionts can benefit from a light feeding regime alongside the base dressing of organic fertilizer in the compost. This is effective if given through the foliage, using balanced foliar feeds (with equal proportions of nitrogen to potassium and phosphate) throughout the period of growth at half the recommended strength for other plants.

Frequency of feeding depends on the subject and the time of year. Winter-growing orchids may be fed fortnightly during the shorter days, increasing the rate to weekly in longer days, until growth ceases. Summer-growers may be fed weekly from the time their leaves are fully developed until they begin to fade.

PESTS

Pests divide into two categories: biting and chewing, such as slugs, snails, and weevils; and sucking, including aphids, mealy bugs, scale insects, and mites. The chemical controls recommended are safe to use on orchids, as long as the manufacturers' instructions are followed strictly. Active ingredients have been listed wherever possible rather than brand names, which may vary from time to time and country to country. All spraying and other operations must be carried out in accordance with instructions on the label. Avoid spraying when the plants are under stress, particularly in hot sunny weather. Bright (but not sunny), buoyant conditions are best.

CHEWING AND BITING PESTS

Slugs and snails: Leave tell-tale slime trails. Control: baits, powders or drenches of metaldehyde of methiocarb. Drenches may affect mycorrhizae.

Cockroaches: Nocturnal, often attacking young shoots, flowers or root tips. Control: gamma-BCH, permethrin, deltamethrin (these controls also apply to other beetles).

Thrips: Small black insects that can cause fine stippling on the upper sides of foliage. Control: malathion, gamma-BCH, diazinon, dimethoate.

Fungus gnats: Small larvae attack soft seedlings and break down composts based on peat. Control: gamma-BCH, pyrethrum-based insecticides.

Weevils: Attack leaves causing semi-circular holes in the edges (vine weevils). Their larvae may also attack tubers in the soil. Control: gamma-BCH.

SUCKING PESTS

Aphids: attack soft growth and inflorescences. Can spread viruses; control when first seen. Control: derris, pyrethroids, malathion, pirimicarb, dimethoate.

Mealy bugs: a problem with warmer-growing orchids, evergreens in particular. Covered in white mealy wax. Control: malathion, dimethoate, deltamethrin, with a wetting agent to increase effectiveness.

Scale insects: mainly affecting warmer-growing evergreen species. May be soft-bodied or hard, and whitish, brown or black. Control: immature stages by using malathion and deltamethrin; adults by malathion and dimethoate.

Whitefly: A problem late in the season of growth of some winter-growing species. Control: smokes of pirimiphor-methyl.

(All the above pests secrete 'honeydew', on which black sooty mould may grow; this is one of the first signs of infestation.)

Red spider mites: Worse on thin-leaved orchids; very small, causing fine stippling under leaves or silvery webbing over plants. Control: derris, pyrethroids, dimethoate.

OTHER PESTS

Worms: Can ruin the structure of compost in a pot. Flush out by watering with pyrethrum, at the usual rate for control of aphids.

Mice: May attack tubers and young growths. Control with traps and baits.

Eelworms: Reported on *Dactylorhiza*. Infected plants may show pale streaking and flecking of leaves and distortion of the roots and tubers. No control available to amateurs. Buy only healthy stock; discard infected plants and the compost or soil in which they were growing. Eelworms spread in soil moisture or that present around the base of the pots. Growing on slatted staging will help to prevent this.

Diseases

These are caused primarily by fungal and bacterial pathogens. Viruses, although rarer, are potentially damaging to orchids. They are often spread by poor cultural practices.

Virus diseases

Viruses occur mainly in genera such as *Dactylorhiza* with a history of vegetative propagation. Infection is often spread in sap by handling and cutting into plant tissue. Main symptoms are colourless or black patterning or streaking of leaves (chlorotic or necrotic, respectively). Growth may be poor, and flowers may be distorted or with brown necrotic patches. There are no controls, so discard infected plants. Sterilize all cutting tools with a propane torch or by soaking in 10% trisodium orthophosphate.

Bacterial rots

Bacterial rots may occur spontaneously or infect through damaged tissue. A common symptom is soft brown areas, accompanied sometimes by an offensive smell. Control can be by cultural means: cut off affected tissue, avoid close stagnant conditions, and do not allow water to lodge in growths overnight or during cold weather. Bactericides such as quaternary ammonium compound (marketed as Physan) will slow or stop the spread, as will drying off or placing plants in a strong airstream.

Fungal diseases

These divide into two types, rots and 'dry' diseases such as rusts. Rots are prevalent in still conditions. Leaf, stem, rhizome, and tuber rots are often characterized by a purple stain produced in the leading edge of the infected area. Control by cutting off all infected areas of tissue and spraying or dipping the plant in Physan. Root rots are usually associated with poor aeration and drainage in the potting medium. Repot affected plants after removing affected tissues. Control of fungal conditions of symbiotically grown terrestrials is best effected by sprays of the (usually above-ground) infected parts with non-systemic fungicides such as Physan, but occasionally systemic remedies are essential to save the plant in question. Carbendazim is an effective broad-spectrum systemic fungicide.

Tuberous terrestrials may suffer from a systemic fungal condition, showing in the foliage as black streaking and spotting, gradually moving back into the stem and tuber. Once the infection has spread to the stem of the rosette, death often follows; above-ground parts must be cut off to save the tuber. Annual repotting and growing on slatted or mesh benches reduces the occurrence of this condition.

Rust fungi produce orange-red pustules on foliage and stems. Control by destroying affected parts and spraying generally with ferbam or zineb as a preventative. Other leafspot fungi may cause small sunken spots, perhaps with a purple-black line around the edge. Control with sprays of mancozeb. Leaf dieback from the tips (if caused by fungi) will be controlled by copper preparations or mancozeb. Cultural leaf-tip dieback may be caused by lack of trace elements; ensure plants have a proper feeding regime.

Grey mould (*Botrytis*) usually occurs on dead tissue but can spread to living parts and may cause brown spotting of flowers. Control by ensuring good air movement and refrain from spraying over plants in dull humid weather. For leaf and stem infections, cut off affected parts and dust cut surfaces with sulphur or carbendazim. Flower infections are usually cured by cultural means. Severe infections may require Benomyl treatment.

Propagation

Generally, orchids multiply slowly in cultivation. Most Orchideae are tuberous terrestrials, producing one or more replacement tubers with each growth cycle. Some have short rhizomes with root tubers and may be propagated by division. Propagation from seed by aseptic and 'symbiotic' techniques requires sophisticated equipment not used by many gardeners and will not be dealt with here. The traditional practice of sowing seed around a 'mother plant' to take advantage of the symbiotic fungus associated with it is worth trying, but it is only occasionally successful. A few genera have species which can be described as 'weeds' of cultivation. Some *Cynorkis* and *Dactylorhiza* species can spread by seed in the greenhouse or garden respectively, appearing spontaneously in pots or wherever conditions are suitable. While often welcome, this is not a dependable means of increase.

The appearance of the tubers may vary considerably, as does their ability to reproduce vegetatively. Species in some genera (e.g. *Serapias*) are vigorous colony-formers, dropping numerous tubers toward the bottom of a container, with tubers and growths sometimes emerging through drainage holes. *Dactylorhiza* species may quite rapidly form clumps, each plant giving rise to a number of new tubers of various sizes, typically immediately below the rosette. Many *Ophrys* species, however, rarely form more than one tuber each year.

For most genera the main replacement tuber or tubers develop immediately below the rosette and are mature by flowering time. The simplest means of propagation is to divide the tubers at any time during the dormancy of deciduous species or just as new growth begins with evergreen species. All divisions must retain a growth bud at the apex and are grown on in the same way as the original plant.

Where more rapid increase is required, plants can be coaxed into producing extra tubers by removing the new tuber at the correct stage of development. This removes the hormonal influence it exerts to suppress the growth of dormant axillary buds into tubers. There are two techniques, described as 'summer' and 'winter' propagation. Developed with European species, their names are based upon the seasonal growth patterns of plants from that area. They work equally well with tuberous genera from else-where at the same stages in their growth cycles as described below.

Summer propagation is used as the flowers fade (from early spring onwards, depending on species and conditions). Remove the plant from the ground or pot and separate the new tuber from the rosette by cutting the stolon joining them, or if none is visible, at the point of attachment. The rosette and old tuber, with most of the root system intact, is planted or repotted as normal, as is the new tuber.

Aftercare of the two differs. Treat the new tuber as if dormant. The flowered shoot and old tuber should be kept in growth for as long as possible to allow new tubers to develop before dormancy. Do not allow seed set. Shady, moist conditions may help to delay dormancy. After the rosette has died down, give normal dormancy conditions, and thereafter treat any new tubers normally.

Winter propagation uses the unflowered rosette at the stage of growth that winter-growing species reach around mid-December in the northern hemisphere, several months into their growth cycle. By this time, many species will have a fully developed rosette, with a developing replacement tuber. Remove the new growth from the old tuber, making the cut toward the bottom of the stem to which it is attached, leaving a small portion with some roots still attached to the old tuber. As both pieces will be grown on normally, the operation may be performed without the plant being removed from its pot. If that is difficult to achieve, remove the plant from its pot, propagate, and grow on the two pieces separately.

The original rosette should flower as normal and produce a replacement tuber. The old tuber should develop one or perhaps two new growths from dormant axillary buds on the small piece of stem left when the rosette was removed, with new tubers appearing in due course. Normal growing conditions and dormancy can be given. Tuberous terrestrials may be propagated by this method at whatever time of year they reach the appropriate stage of growth.

Some genera are characterized by short rhizomes with fleshy roots rather than tubers (e.g. *Stenoglottis* and *Galearis*). These may form small clumps that can be lifted and divided. They may be divided at any time during dormancy but optimally as the growth cycle begins. Treat normally after division.

Specific recommendations

Species of Orchideae have a patchy record at best as cultivated plants, perhaps solely in botanic gardens, as they have been mainly of research interest. However, those commercially available as artificially propagated plants should grow well in cultivation following the methods described here. Do *not* remove mature plants or seed capsules from the wild, as the plants are likely to die and natural populations suffer. Composts are suggested for specific genera below, with the caveat that original habitat details will provide the best guide. **(CB)**

Taxonomic notes

Senghas (1973–1974) recognized four subtribes in the tribe Orchideae: Androcorycinae, Orchidinae, Habenariinae, and Huttonaeinae. Both Huttonaeinae and Androrycinae are monospecific, but the majority of genera fall into either Orchidinae or Habenariinae, which are distinguished mainly by their stigma morphology. Orchidinae have concave unstalked stigmas, often with confluent lobes, whereas Habenariinae have stalked convex stigma lobes that are usually distinct. He recognized several genera that we have synonymized, including *Parhabenaria* (into *Pecteilis*), *Arnottia* (into *Cynorkis*), *Gymnadeniopsis* (into *Platanthera*), and *Tsaiorchis* (into *Diphylax*).

Dressler (1981) pointed out the equivocal position of *Herminium*, which Vermeulen (1977) considered close to *Platanthera*. Szlachetko (1991) established a monospecific Herminiinae, but we consider this to be a case of taxonomic inflation. On the basis of its known natural hybridization with species of other genera in Orchidinae (*sensu* Dressler 1981), it seems related to these genera. Dressler (1993) also indicated the difficulty of correctly placing *Androcorys*, known from limited material. We include it within a broadly defined Orchidinae until molecular evidence of its affinity is available.

In practice the placement of many genera within Orchideae has proved difficult to determine. The presence or absence of stalked stigmas can be difficult to determine in many genera, especially in preserved material. In reality there appears to be a continuum from taxa with concave sessile stigma lobes to those with stalked convex ones. The limited molecular data available for 'Habenariinae' appear to confirm the blurring of the boundary between subtribes Orchidinae and Habenariinae (Bateman *et al.*, this volume). As it is the hypothesis that best fits current data we, therefore, sink the latter into a more broadly defined Orchidinae. Kurzweil and Weber (1992) also suggested abandoning the recognition of Orchidinae and Habenariinae if it is not supported by new characters, although recent molecular data (Douzery *et al.* 1999) uphold the distinction. We have divided the genera into two artificial groups that correspond to Dressler's Orchidinae (Group 1) and 'Habenariinae' (Group 2) on the basis of their stigma structure. **(PC, HK, PL)**

SUBTRIBE ORCHIDINAE

Orchidinae. Dressler & Dodson, *Ann. Missouri Bot. Gard.,* **47**, 35. Type: *Orchis* L.

Subtribe Angiadeniinae Parl., *Fl. Ital.*, **3**, 418 (1858). Type: *Angiadenia* Parl. (= *Gymnadenia*)

Subtribe Gymnadeniinae Parl., *Fl. Ital.*, **3**, 393 (1858), as '*Gymnadenieae*'. Type: *Angiadenia* Parl. (= *Gymnadenia* R.Br.)

Subtribe Habenariinae Benth. in Bentham & Hooker f., *Gen. Plant.*, **3**, 464, 486 (1883). Type: *Habenaria* Willd.

Subtribe Ophrydinae Benth. & Hook.f., *Gen. Pl.*, **3**, (1883), as '*Euophrydinae*'. Type: *Ophrys* L.

Subtribe Androcorydinae Schltr. in *Notizbl. Bot. Gart. Berlin-Dahlem*, **9**, 568 (1926). Type: *Androcorys* Schltr.

Subtribe Serapiadinae Benth., *J. Linn. Soc. Bot.*, **18**, 288 (1881). Type: *Serapias* L.

Subtribe Platantherinae Schltr., *Notizbl. Bot. Gart. Berlin-Dahlem*, **9**, 568 (1926), as '*Platanthereae*'. Type: *Platanthera* Lindl.

Subtribe Bartholinae Szlachetko, *Fol. Geobot. Phytotax.*, **26**, 316 (1991). Type: *Bartholina* R.Br.

Subtribe Herminiinae Szlachetko, *Fol. Geobot. Phytotax.*, **26**, 320 (1991). Type: *Herminium* R.Br.

Description

Terrestrial or rarely epiphytic *plants* with tubers, rarely mycotrophic with leaves reduced to colourless sheaths. *Root tubers* ovoid, spherical, ellipsoidal or cylindric-fusiform, solitary or in clusters, hairy or glabrous. *Leaves* spirally arranged, one to many, basal or arranged along the stem, deciduous or rarely persistent for more than one year, often sheathing at the base, the lowermost one to several reduced to sheaths, the uppermost often bract-like, usually green, rarely spotted, rarely purple-spotted or shaded beneath. *Inflorescence* terminal, erect or arching, one- to many-flowered, rarely secund; peduncle usually terete, glabrous or less frequently hairy or glandular; bracts linear, lanceolate, ovate or elliptic, sometimes cucullate, usually glabrous and green. *Flowers* small to large, usually resupinate, often showy, green, white, yellow, pink, purple or red; pedicel usually short, often obscure; ovary distinct, glabrous or less frequently hairy or glandular. *Dorsal sepal* free or often adnate to the petals to form a hood over the column. *Lateral sepals* usually free, rarely connate to the base of the column, lip, stigma lobes or rostellum. *Petals* entire or two-lobed. *Labellum* usually lowermost in flower, usually deflexed, entire, three- or five-lobed, less commonly bipartite, occasionally callose, usually spurred at the base; spur saccate, scrotiform, fusiform, clavate or cylindrical, rarely fused to the ovary. *Column* basifixed, rarely adnate to the other floral segments at the base, erect or decumbent; anther bilocular, locules either adnate or separated on a more or less broad connective; pollinia two or four, sectile, attached by short to elongate caudicles to one or two viscidia; lateral appendages (staminodes, auricles) two, usually present, sessile or stalked, usually shorter than the column, rarely filiform and as long as or longer than the column; stigma entire or two-lobed, sessile or stalked, concave to convex; rostellum usually three-lobed, sometimes obscure, the mid-lobe erect or porrect, lying between or in front of the anther loculi, the side lobes short to long, porrect, rarely incurved or upcurved. **(PC)**

Artificial key to subtribe Orchidinae, Group 1 (PC, JW)

1. • Viscidium 1 or 2, naked 2
• Viscidium 1 or 2, surrounded by 1 or 2 bursicles 13

2. • Lip divided into a boat-shaped or long-spurred hypochile and an undivided to tripartite epichile; petals fused at base with column base; plants autotrophic or mycotrophic .... **65. *Brachycorythis***
• Lip lacking a hypochile, entire or divided into 3; plants autotrophic 3

3. • Plants with one or two basal hairy leaves; inflorescence axis hairy; lip and often petals divided into several lacerae 4
• Plants more or less glabrous; lip and petals not usually lacerate; lip side lobes occasionally lacerate but then petals entire or bilobed 5

4. • Inflorescence 1 flowered; lip more than 2 cm long, deeply lacerate .... **62. *Bartholina***
• Inflorescence multi-flowered; lip much shorter than 2 cm .... **82. *Holothrix***

5. • Lip lacking a spur, flat or obscurely saccate at base 6
• Lip spurred or prominently saccate at the base 7

6. • Petals connate to the column in the basal part, adnate to the dorsal sepal and forming a hood over the column; stigma lacking a sterile process at the base .... **84. *Neobolusia***
• Petals free from the column and dorsal sepal; stigma with a sterile basal process .... **74. *Dracomonticola***

7. • Lateral appendages clear and elongate; caudicles of pollinia almost absent .... **58. *Amitostigma***
• Lateral appendages small, unremarkable or clear but then round to ellipsoid 8

8. • Rostellum with very obvious mid-lobe between the anthers 9
• Rostellum lacking an obvious mid-lobe or with a small swelling between the anthers 12

9. • Lip with 3 calli at the base, the 2 lateral near the edge, entire .... **99. *Schizochilus***
• Lip lacking such basal calli, variously shaped 10

10. • Inflorescence secund, rarely 1 flowered; lateral sepals helmet-shaped with the dorsal and petals connate; plant with 1 or 2 basal leaves .... **86. *Neottianthe***
• Inflorescence not secund 11

11. • Flowers small, campanulate, white .... **97. *Pseudorchis***
• Flowers usually larger, usually pink, purple or maroon, not bell-shaped, resupinate or non-resupinate .... **77. *Gymnadenia***

12. • Lip long and tongue-like, pendent, at the base with two side keels and a middle keel which together with the two transverse lamellae nearly closes the entrance to the spur .... **71. *Dactylorhiza*** (***D. viridis***)
• Lip entire or three-lobed but lacking side keels and transverse lamellae at the base .... **93. *Platanthera***

13. • Leaves grass-like in a basal tuft .... **67. *Chamorchis***
• Leaves not grass-like 14

14. • Rostellum broad, concave, jutting out; bursicles formed from the incurved front ends of the side lobes of the rostellum and the inner surfaces of the lengthened anther canals .... **79. *Hemipilia***
• Rostellum small, usually as a narrow, high fold; bursicles formed from the rostellum 15

15. • Lip lacking a spur 16
• Lip spurred or saccate 19

16. • Lip linear, much smaller than sepals .... **56. *Aceratorchis***
• Lip tongue-shaped, 3-lobed or insect-like 17

17. • Column with an extended connective apex; sepals forming a hood; lip mid-lobe tongue-like with two basal ridge-like calli in the throat .... **100. *Serapias***
• Column lacking an extended apex or only exceptionally with a short apex to the anther connective; lip not as above 18

18. • Lip entire or 3-lobed, often insect-like and hairy; sepals not helmet-shaped hood .... **88. *Ophrys***
• Lip not insect-like; sepals often forming a helmet-shaped hood over the column .... **89. *Orchis*** (in part)

19. • Pollinia connected to a common viscidium 20
• Pollinia with 2 viscidia 23

20. • Plants with fleshy thickened roots .... **68. *Chondradenia***
• Plants with root tubers 21

Artificial key to subtribe Orchidinae, Group 1 (PC, JW) (*cont'd*)

21. • Lip mid-lobe elongated or at least much longer than broad .... **81. *Himantoglossum***
• Lip mid-lobe not as above 22

22. • Lip 3-lobed with an entire mid-lobe, with two parallel keels at the base .... **59. *Anacamptis*** (in part)
• Lip 3-lobed with a divided mid-lobe, lacking basal calli .... **61. *Barlia***

23. • Sepals fused for at least two-thirds of their length 24
• Sepals separated 25

24. • Spur very short, deeply notched almost double-spurred .... **103. *Steveniella***
• Spur as long as the lip, with a horseshoe-shaped callus in front of mouth of spur .... **104. *Symphyosepalum***

25. • Viscidia with distinct bursicles 25
• Viscidia with a common bursicle 28

26. • Plants with short to elongate rhizomes .... **75. *Galearis***
• Plants with rounded or elongate tubers 27

27. • Bursicles cannot be folded downward, with a fine membrane; tubers elongated, usually one-leaved .... **95. *Ponerorchis***
• Bursicles distinct, can be folded down; tubers roundish; leaves several on the stem .... **106. *Traunsteineria***

28. • Plant with digitate tubers or with rhizome 29
• Plant with round tubers 30

29. • Plant with digitate tubers; stigma entire; stem with several leaves .... ***Dactylorhiza*** (except ***D. viridis***)
• Plant rhizomatous; stigma entire but side parts divergent in a V-shape; stem with 1 leaf, rarely 2 .... **57. *Amerorchis***

30. • Stigma depression not entire but with 2 ascending lobes .... **85. *Neotinea***
• Stigma depression entire, round or trapeze-shaped 31

31. • Petals strongly dentate; lip elongated into 4 thread-like tips .... **69. *Comperia***
• Petals entire; lip entire or 3-lobed with the mid-lobe sometimes deeply emarginate to give a 4-lobed appearance, often apiculate in the sinus of the mid-lobe. 32

32. • Leaves basal, usually in a rosette; flowers yellow or, if purple or pink, often with tufts of hairs on the lip; lip usually 4-lobed; dorsal sepal usually erect .... **89. *Orchis***
• Leaves basal and cauline and sheathing; flowers predominantly purple or pink; lip entire or 3-lobed; dorsal sepal usually hooded over column .... **59. *Anacamptis*** (in part)

Artificial key to subtribe Orchidinae, Group 2 (Habenariinae sens. auct.) (PC)

1. • Stigma(s) sessile, always convex, the whole protruding out of the stigmatic area, sometimes incompletely divided or completely divided 2
• Stigmas stalked 11

2. • Plants rhizomatous 3
• Plants with swollen, tuberous roots 4

3. • Flowers non-resupinate, orange-red; lip lacking a callus .... **101. *Smithorchis***
• Flowers resupinate, white, with basal fleshy callus .... **108. *Veyretella***

4. • Lip flat or possibly concave at base, rarely obscurely saccate 5
• Lip spurred or prominently saccate at base 8

5. • Lip auriculate at base, with two glands at the base; stigma entire; rostellum relatively large .... **96. *Porolabium***
• Lip not auriculate at base, lacking glands; stigma 2-lobed; rostellum obscure 6

6. • Lip usually 2- to 3-partite, also 5-dentate; flat or slightly depressed at the base .... **80. *Herminium***
• Lip entire 7

7. • Lip usually depressed or slightly saccate at base; plants from Asia .... **60. *Androcorys***
• Lip usually with a 4-sided depression at the base with a little dimple in front; plants from Madagascar .... **107. *Tylostigma***

8. • Anthers with broad connective, the canals elongated; flowers large (diameter < cm); spur elongated .... **90. *Pecteilis***
• Anthers with narrow connective, canals short; flowers small (diameter <1 cm); spur short, rarely as long as the ovary; lip usually neither noticeable nor longer than the perianth 9

Artificial key to subtribe Orchidinae, Group 2 (Habenariinae sens. auct.) (PC) (*cont'd*)

9. • Lateral appendages as long as the column, filamentous or slender with a clavate tip; stigma entire . . . . **72. *Diphylax***
• Lateral appendages shorter than the column, usually sessile; stigma bilobed 10

10. • Lip with a small callus of 1–3 swollen ridges at base of lip in mouth of spur; stigma lobes separate and fused to the base of the edge of the lip and to the staminodes . . . . **91. *Peristylus***
• Lip ecallose; stigma lobes not fused 11

11. • Swollen roots fasciculate; leaves linear to lanceolate, not as below; petals narrower than sepals . . . . **63. *Benthamia***
• Swollen roots ellipsoidal to ovoid, not fasciculate; leaves several, ovate with marked reticulate venation, in a basal rosette; petals broader than sepals . . . . **87. *Oligophyton***

12. • Lip lacking a spur; rostellum very reduced 13
• Lip with a basal spur 14

13. • Lateral appendages stalked, club-shaped, roots thickened, clustered; leaves many, in a rosette; lip 3–5 lobed . . . . . . **102. *Stenoglottis***
• Lateral appendages small, sessile; roots 1–2, thickened; leaves 1–2, basal; lip entire, rarely or occasionally with a short side tooth . . . . **70. *Cynorkis*** (in part)

14. • Spur fused to the ovary for entire length; lip with a verrucose basal callus . . . . **105. *Thulinia***
• Spur free from ovary; callus, if present, simple 15

15. • Lateral appendages as long as the column . . . . **76. *Gennaria***
• Lateral appendages shorter than the column, often sessile 16

16. • Stigma lobes long, divided into an upper usually sterile and a lower sturdier fertile branch 17
• Stigma lobes short or long, entire 18

17. • Lip fused with column; connective very narrow and high; anther parts parallel . . . . **66. *Centrostigma***
• Lip free from column; connective broader and lower; anther parts diverging outward . . . . **98. *Roeperocharis***

18. • Rostellum mid-lobe plate-shaped, porrect, overtopping the anthers; stigma lobes connected by membrane; lip entire, flabellate with a small apicule . . . . **73. *Diplomeris***
• Lacking this combination of characteristics 19

19. • Growth with an oval leaf in middle of stalk, surviving several seasons; spur short, bladder-shaped, grooved; anther canals 2 lobed at front and covering the viscidia . . . . **92. *Physoceras***
• Leaves different; anther canals without terminal lobes 20

20. • Column very low with very broad connective; anther parts almost horizontal; canals folded outward and backward so that the viscidia do not face the lip . . . . **83. *Megalorchis***
• Column different; anther parts more or less vertically orientated; viscidia lie in front of spur opening 21

21. • Petals deeply bifid; lateral sepals, lip and anterior lobe of petals fused to the long stigma lobes; lip with a callus mound in front of spur opening . . . . **64. *Bonatea***
• Petals usually entire, if not bifid but not fused to the other organs; lip lacking a callus 22

22. • Petals always entire; lip usually entire, sometimes slightly 3 dentate in middle; lateral sepals strongly recurved; inflorescence few flowered, lacking glands; stigma lobes long and clavate, not fused with rostellum . . . . **94. *Platycoryne***
• Plants with other combination of characters 23

23. • Petals always entire; inflorescence often glandular and hairy; flowers usually pink or purple; lip entire or up to 5 dentate, if deeply divided then never with linear or thread-like tips; anther canals fused with sides of rostellum; leaves usually basal, often only 1 or 2; plants from Afro-Madagascan region . . . . **70. *Cynorkis*** (in part)
• Petals often bifid; inflorescence rarely glandular and hairy; pink or purple flowers absent in Afro-Madagascan species; lip usually deeply divided, seldom entire, often with linear or thread-like tips; anther canals usually not fused for full length with sides of rostellum; leaves usually many, rarely basal (except in sect. *Diphyllae*), usually more or less regularly spread over stem . . . . **78. *Habenaria***

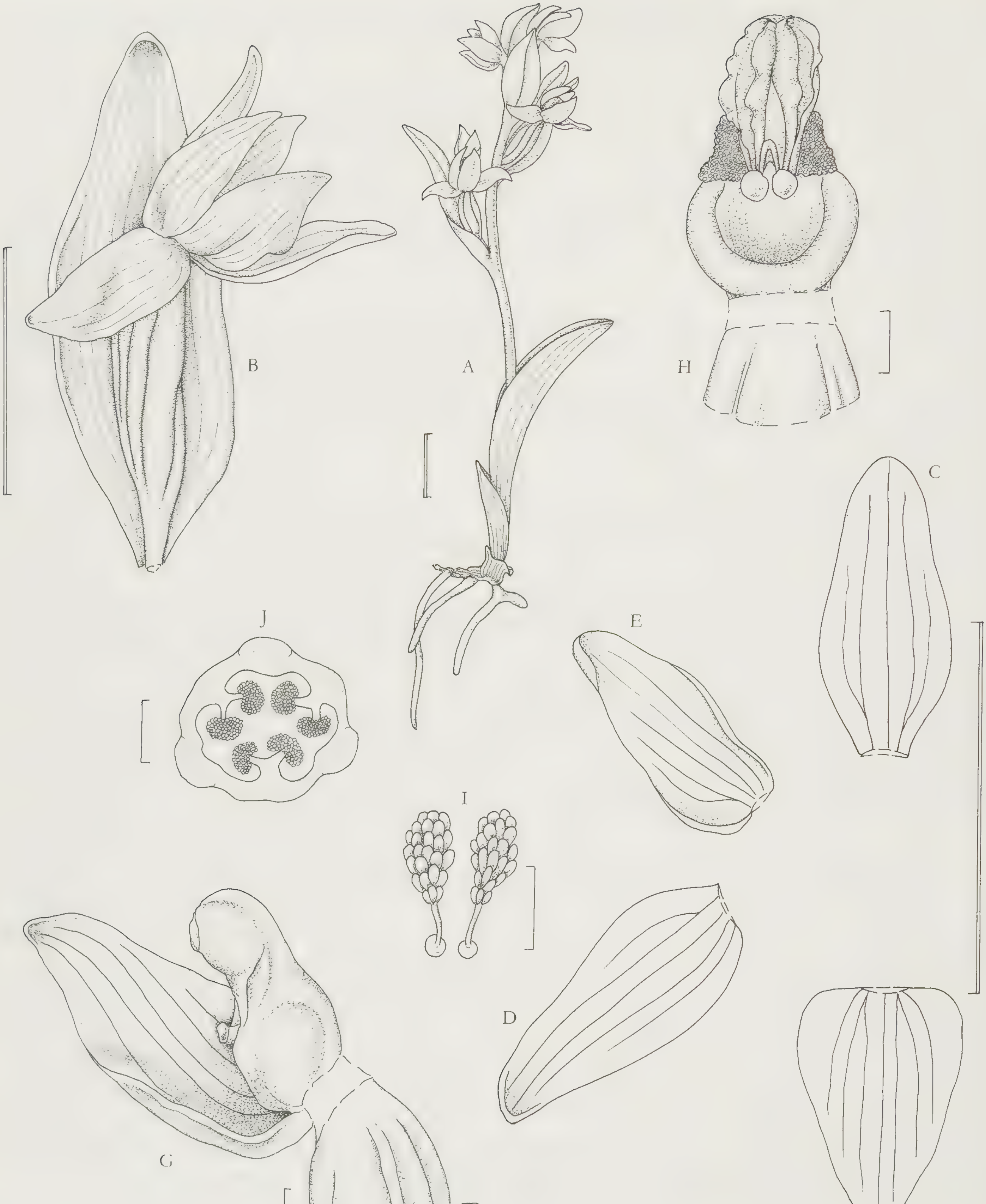

Fig. 56.1. *Aceratorchis tschiliensis* Schltr. A. Habit; B. Flower and bract; C. Dorsal sepal; D. Lateral sepal; E. Petal; F. Labellum; G. Labellum and column, side view; H. Column, front view; I. Pollinaria; J. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Rock 14190* (K) and Kew Spirit Collection no. 56708.

56. ACERATORCHIS

Aceratorchis Schltr., *Feddes Repert. Beih.*, **12**, 328 (1922). Type not designated.

Derivation of name

From the Greek *akeratos*, without a home, and *orchis*, an orchid, in allusion to its spurless, entire lip. **(PC)**

Description (Plate 75; Fig. 56.1)

Perennial, rhizomatous *herbs*. *Rhizome* stolon-like. *Tubers* absent. *Stem* with two cataphylls. *Leaves* basal, solitary (rarely two), petiolate; lamina elliptic or oblong-elliptic, obtuse, fleshy, unspotted. *Inflorescence* few flowered, erect, terminal; peduncle naked; rachis short; floral bracts leafy, longer than flowers. *Flowers* resupinate, purple with white area on lip, or white. *Sepals* and *petals* connivent, forming a hood, ovate-oblong to elliptic-oblong, obtuse. *Labellum* entire, ligulate, entire, lacking a spur. *Column* short; stigma two-notched; rostellum distinct; anther ellipsoid, loculi parallel; pollinia two, attached to a solitary viscidium enclosed in a well-formed or indistinct bursicle. *Ovary* twisted, sessile. *Capsule* cylindrical. **(JW/PC)**

Distribution (Fig. 56.2)

A genus of two species endemic to China (Xizang, Hebei, Shanxi, Sichuan, Qinghai). **(JW/PC)**

Ecology

Plants of *Aceratorchis* grow in alpine meadows, steep gritty pastures, grassy slopes facing south, and on shady rocks between about 3000–4500 m. **(JW)**

Uses

None recorded. **(JW)**

Cultivation

Little-known in cultivation. Compost C or D. **(CB)**

Taxonomic notes

Aceratorchis was established by Schlechter in 1922. Flowers of *A. tschiliensis* have a petaloid, spurless labellum and may be peloric in this respect. The genus needs to be compared with *Galearis* and other rhizomatous members of the tribe. **(JW/PC)**

57. AMERORCHIS

Amerorchis Hultén, *Ark. Bot.*, ser. 2, **7**, 34 (1968). Type species: *Amerorchis rotundifolia* (Banks) Hultén.

Derivation of name

Named for America, the type locality of this *Orchis*-like genus. **(JW)**

Description (Plate 76; Fig. 57.1)

Small to medium-sized *herb*. *Rootstock* fibrous, borne from a slender, branching rhizome. *Stem* scapose, glabrous. *Leaf* solitary, basal, ovate to suborbicular, fleshy, unspotted. *Inflorescence* a lax, up to 15 flowered raceme; floral bracts narrowly elliptic, about 10 mm long. *Flowers* white to pale pink, lip variously marked with purple-red. *Dorsal sepal* and *petals* connivent, forming a hood over column, glabrous. *Lateral sepals* spreading. *Labellum* three-lobed, spurred,

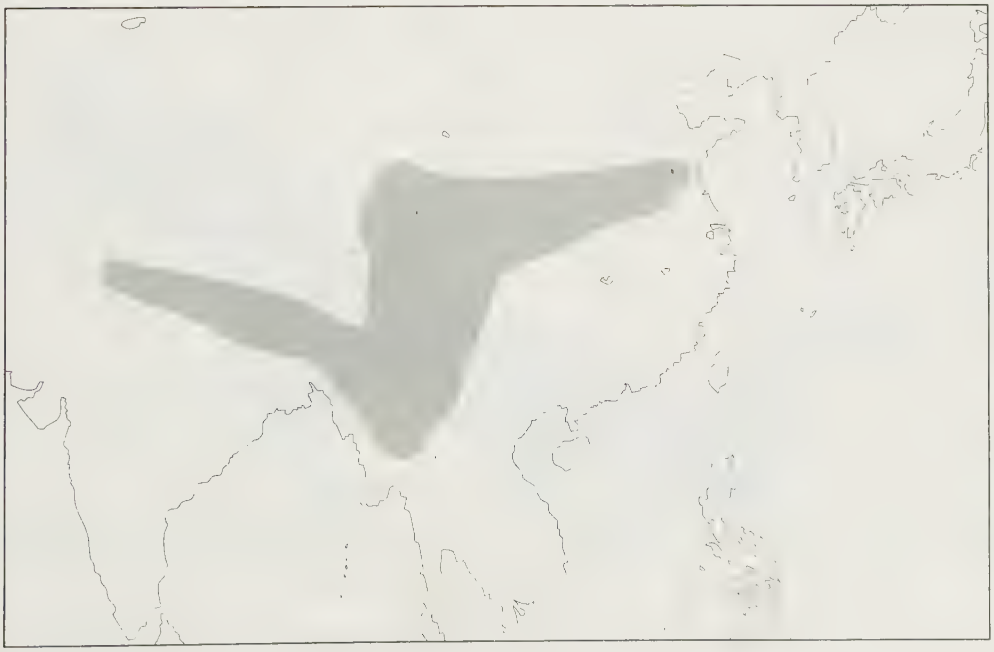

Fig. 56.2. Distribution map of *Aceratorchis*

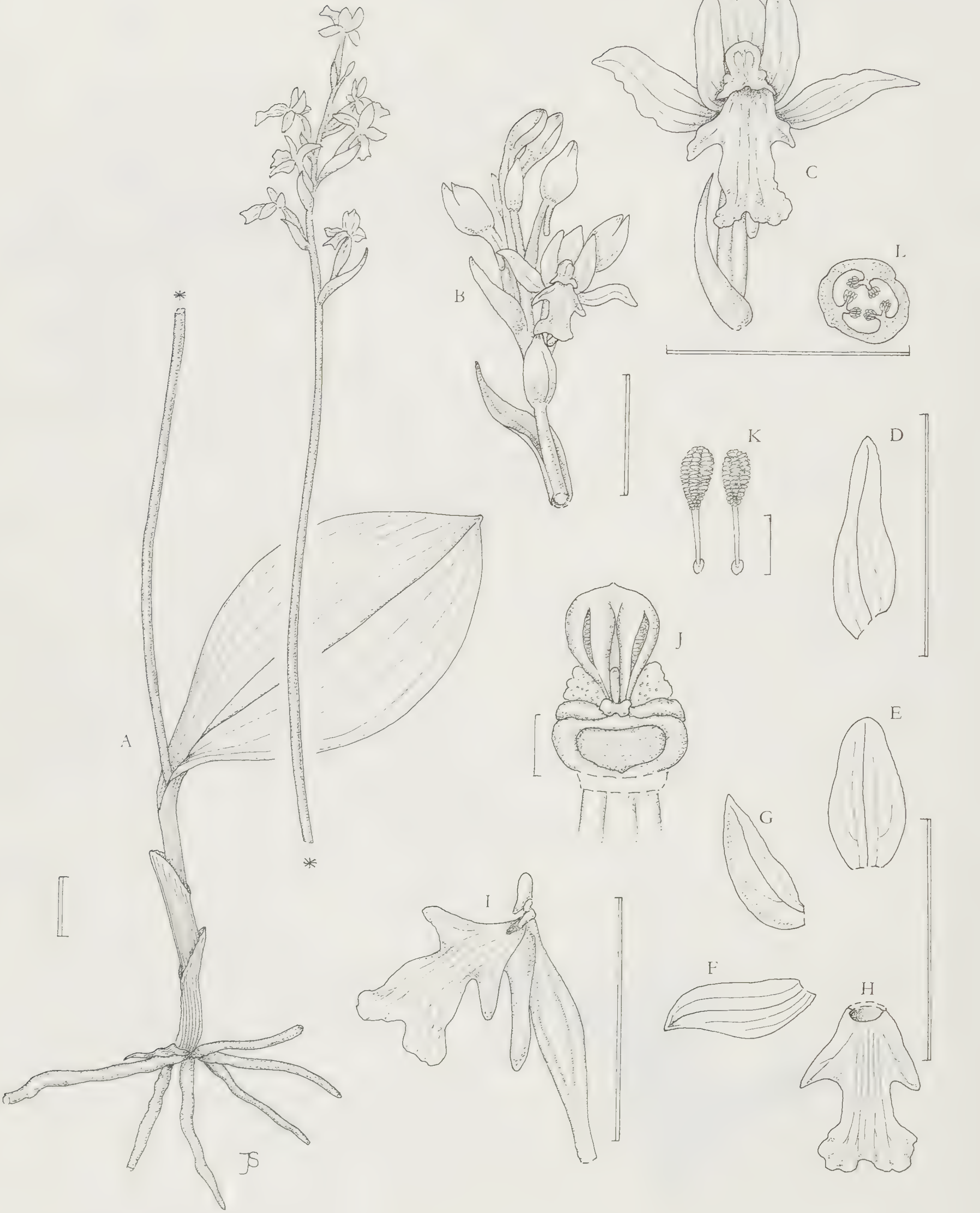

Fig. 57.1. *Amerorchis rotundifolia* (Banks) Hultén. A. Habit; B. Inflorescence; C. Flower; D. Bract; E. Dorsal sepal; F. Lateral sepal; G. Petal; H. Labellum; I. Labellum, spur, and column, side view; J. Column, front view; K. Pollinaria; L. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *McCalla 2235*.

mid-lobe dilated or bilobed, spur slender, decurved. *Column* short, erect; anther loculi parallel, contiguous; pollinia two, viscidia enclosed in a solitary bursicle above orifice to nectary, flanked on either side by a conspicuous stigmatic process. **(JW)**

Distribution (Fig. 57.2)

A monospecific genus distributed across Canada, the northern United States of America, and southern Greenland. **(JW)**

Ecology

Amerorchis rotundifolia is a rhizomatous-stoloniferous terrestrial orchid that grows along streams and in wet, mossy woodland or swamps on calcareous soils with good drainage (Rickett 1966; Hitchcock *et al.* 1969; Scoggan 1978). In Wisconsin in the United States, for example, where it is a rare species at the edge of its range, *A. rotundifolia* is found almost exclusively in calcareous bogs on which white cedar and larch are the dominant species. It is more commonly found in the boreal forest region of northern Canada, which is characterized by large areas of spruce and muskeg (Catling 1984). Fungi forming mycorrhizal associations with *A. rotundifolia* in the field in Canada have been identified as *Epulorhiza calendulina* (Zelmer and Currah 1995). Flowering of *A. rotundifolia* takes place from June through July. In some areas it is under threat from human activities where its woodland habitat is being destroyed by urban expansion (Luer 1984). **(RN)**

Uses

None recorded. **(JW)**

Cultivation

Amerorchis rotundifolia occupies habitats from tundra to conifer forests and shaded bogs in southern areas of range, often growing over lime. Pot in compost C or D. It may be grown in a containerized bog. **(CB)**

Taxonomic literature

Luer, C. A. (1975). *Native orchids of United States and Canada, excluding Florida*. New York Botanical Garden.

58. AMITOSTIGMA

Amitostigma Schltr., *Feddes Repert. Beih.*, **4**, 91 (1919). Type species: *Amitostigma gracile* (Blume) Schltr.

Mitostigma Blume, *Mus. Bot. Lugd.-Bat.*, **2**, 189 (1856), *non* Decne. Type species: *Mitostigma gracile* (= *Amitostigma gracile* (Blume) Schltr.)

Derivation of name

From the Greek α-, not, *mitos*, a thread, and *stigma*, a stigma, a substitution for Blume's *Mitostigma*, a later homonym that had been used earlier by J. Decaisne for a genus of the Asclepiadaceae. **(JW)**

Description (Plate 77; Fig. 58.1)

Perennial *herbs*. *Tubers* small, ellipsoid. *Stem* with two cataphylls. *Leaves* solitary, oblong or narrowly elliptic, acute, unspotted. *Inflorescence* one- to few-flowered, erect, terminal; peduncle naked or with a sheathing sterile bract; rachis short; floral bracts mostly shorter than or equalling ovary. *Flowers* resupinate, white, pink, mauve, purple, or rarely yellow, labellum often with deeper purple markings.

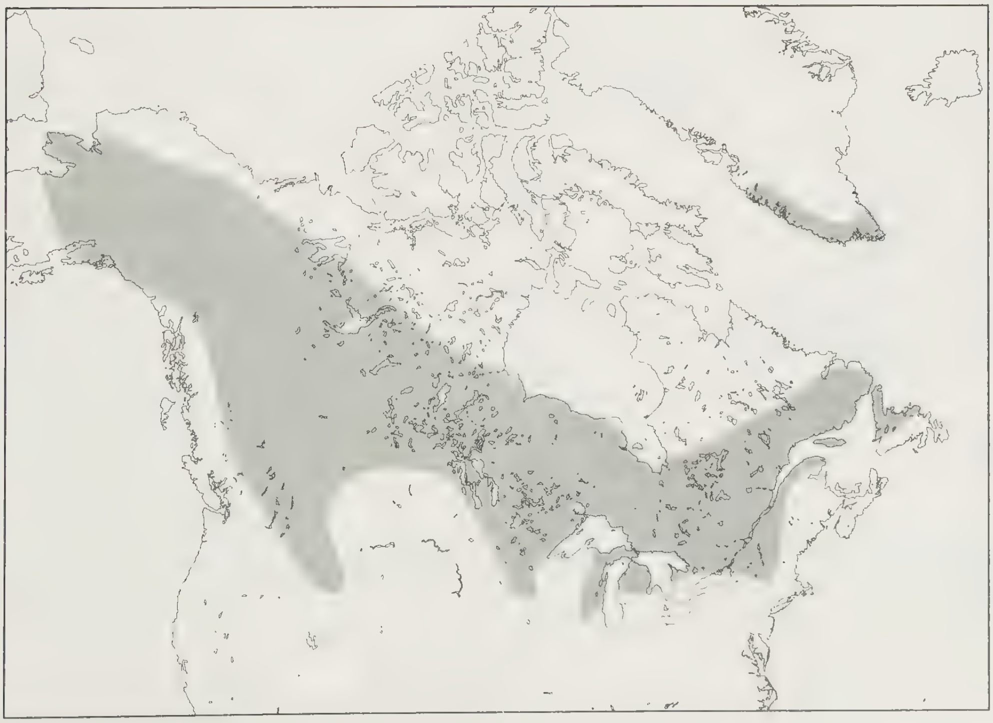

Fig. 57.2. Distribution map of *Amerorchis*.

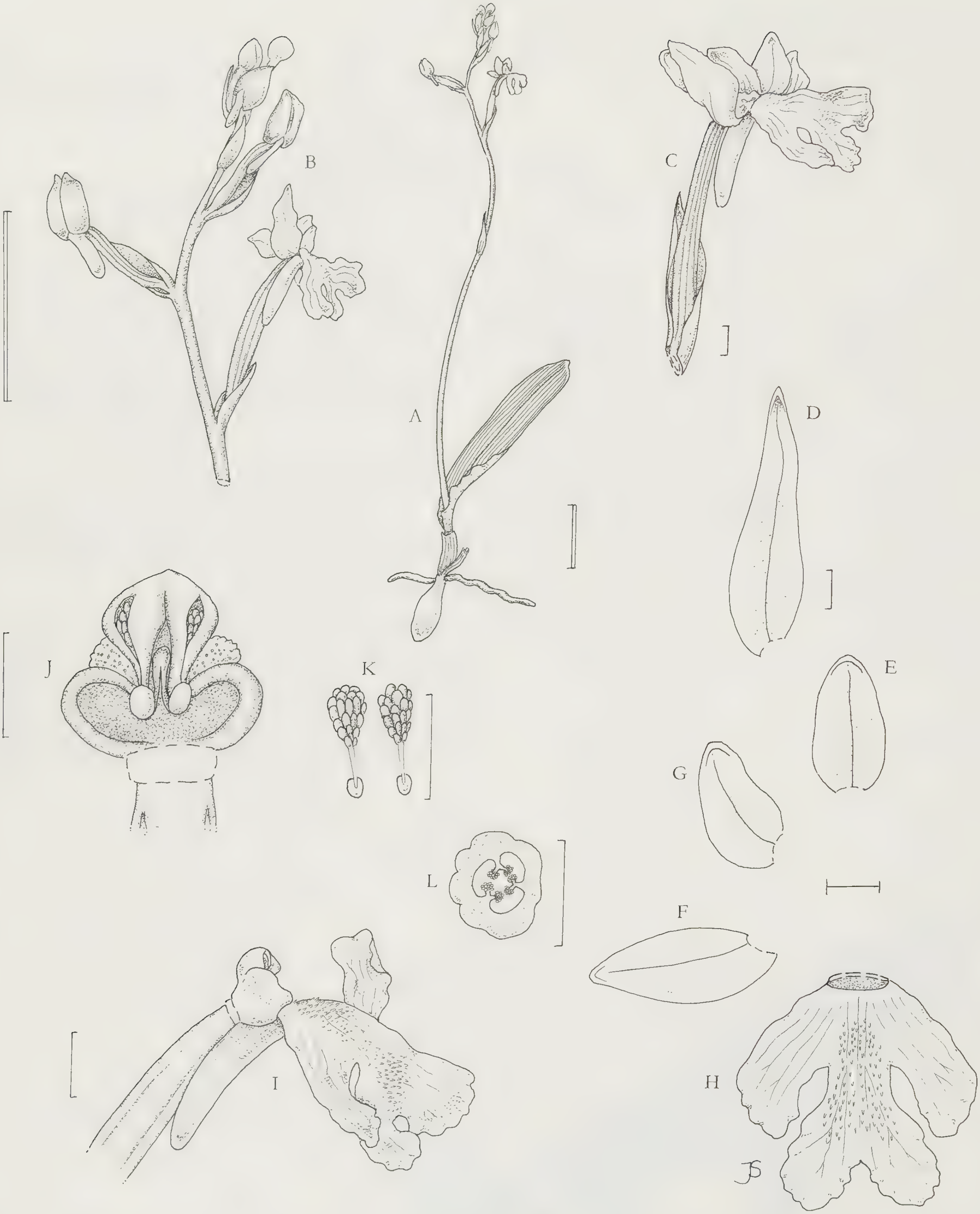

Fig. 58.1. *Amitostigma gracile* Schltr. A. Habit; B. Inflorescence; C. Flower; D. Bract; E. Dorsal sepal; F. Lateral sepal; G. Petal; H. Labellum; I. Labellum, spur, and column, side view; J. Column, front view; K. Pollinaria; L. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Dunn 354* and Kew Spirit Collection no. 61640.

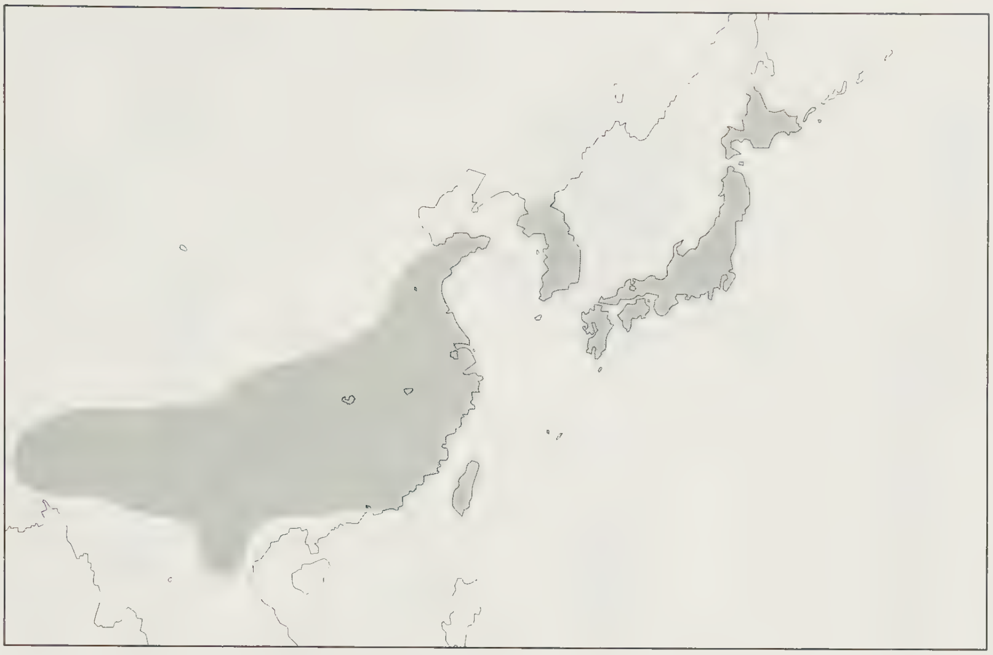

Fig. 58.2. Distribution map of *Amitostigma*.

Sepals and *petals* free, often connivent, obtuse. *Labellum* spurred, variously three-lobed, somewhat cuneate at base, mid-lobe often bilobed, spreading, often with spots or lines on disc, spur cylindrical to narrowly conical, short, or elongate (e.g. *A. pinguicula*). *Column* short; stigma solitary, narrow, sessile, positioned under the anther, with strongly diverging, filiform lateral stigmatic lobes adnate to the lower margins of the labellum; staminodes clear and elongate; rostellum small, low; anther sessile, horizontal, loculi parallel; pollinaria short, pollinia two, subsessile, with minute caudicles sitting directly on naked viscidia; viscidia positioned in roof above spur entrance; bursicles absent; pollen falling loosely in tetrads. *Ovary* sessile or shortly pedicellate. *Capsule* cylindrical. **(JW)**

Distribution (Fig. 58.2)

About 30 species distributed in India (Sikkim), China (including Tibet), Japan, Kurile Islands, Taiwan, Korea, Myanmar, Vietnam and Thailand, the majority occurring in China. **(JW).**

Ecology

Members of the genus *Amitostigma* are terrestrial herbs with tuberous roots, which often grow in mountainous situations among wet, moss-covered rocks next to streams, on shaded rocky cliffs, and in bogs (Ohwi 1965; Rasmussen 1995). In north-west Yunnan, *A. tibeticum* has been observed growing in meadows with other orchids, such as *Cypripedium* species, on the eastern slopes of the Jade Dragon Snow Mountain (Cribb 1994), whereas on Okinawa, *A. lepidum* is reported to be common in fields (Walker 1976). *Amitostigma* flowers between March and August, the exact period varying between species, and the plants are 'summer-green' (Rasmussen 1995). **(RN)**

Uses

None recorded. **(JW)**

Cultivation

Native species of *Amitostigma* are cultivated in East Himalaya, China, and Japan. Woodland treatment, best in greenhouse or shadehouse, compost D. **(CB)**

Taxonomic notes

Amitostigma beesianum and *A. lepidum* have several leaves, requiring further investigation and probable removal from the genus. **(JW)**

Taxonomic literature

Blume, C. L. (1856). *Museum Botanicum Lugdano-Batavum*, **2**, 189.

Brieger, F. G., Maatsch, R., and Senghas, K. (1973). 17. *Amitostigma*. In *Rudolf Schlechter: Die Orchideen 3. Völlig neubearbeitete auflage* (ed. F. G. Brieger, R. Maatsch, K. Senghas), **4** (13–16), 212.

Schlechter, R. (1919). *Orchideologiae Sino-Japonicae Prodromus.* Eine kritische Besprechung der Orchideen Ost-Asiens, 91.

Vermeulen, P. (1972). Übersicht zur Systematik und Taxonomie der Gattung *Orchis* s. str. *Jahresberichte des Naturwissenschaftlichen Vereins in Wuppertal*, **25**, 33.

59. ANACAMPTIS

Anacamptis Rich., *Orch. Eur. Annot.*, **25**, 33 (1817), preprint from *Mém. Mus. Hist. Nat. Paris*, **4**, 47, 55 (1818). Type species: *Anacamptis pyramidalis* (L.) Rich.

Vermeulenia Á. Löve & D. Löve, *Acta Bot. Neerl.*, **21**, 554 (1972). Type species: *Vermeulenia papilionacea* (L.) Á.Löve & D. Löve (= *Anacamptis papilionacea* (L.) R.M. Bateman, Pridgeon & M.W. Chase).

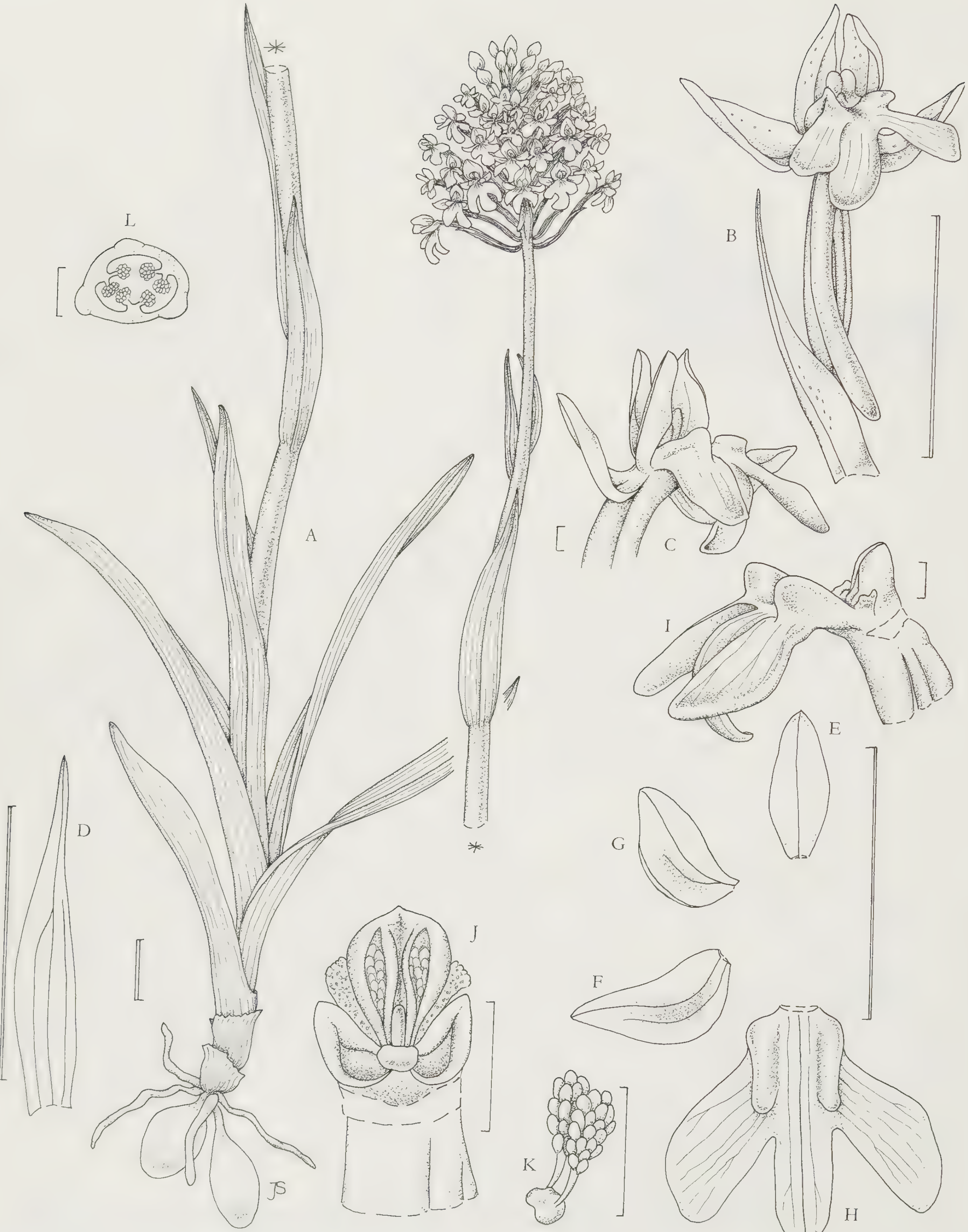

Fig. 59.1. *Anacamptis pyramidalis* (L.) Rich. A. Habit; B. Flower, front view; C. Flower, side view; D. Bract; E. Dorsal sepal; F. Lateral sepal; G. Petal; H. Labellum; I. Labellum and column, side view; J. Column, front view; K. Pollinaria; L. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Busyman s.n.* (K) and Kew Spirit Collection no. 45910.

Derivation of name

From the Greek *ana-*, back, and *kamptein*, to bend, alluding either to the reflexed tips of the floral bracts or to the reflexed pollinia. **(JW)**

Description (Plates 78, 79; Fig. 59.1)

Rootstock tuberous, tubers ovoid, entire. *Stem* glabrous, leafy. *Leaves* basal and cauline, unspotted. *Inflorescence* densely to laxly few to many-flowered, shortly racemose to elongate; floral bracts membranous, sometimes leafy, slightly shorter than, equalling or exceeding ovary. *Sepals* and *petals* usually slightly concave, glabrous, dorsal sepal and petals connivent to form a helmet or hood (galea), or free but forming a loose hood (in *A. papilionacea*), *lateral sepals* spreading. *Labellum* spurred, entire and flabellate, shallowly three-lobed or distinctly three-lobed, side lobes (when present) rounded, oblong-rhombic, obliquely triangular or linear, mid-lobe (when present) entire or bilobed, glabrous, papillose or occasionally hirsute, sometimes with two longitudinal basal calli, spur filiform or broad and thick, entrance sometimes with crests and angular in profile, descending, horizontal or ascending, sometimes nectariferous. *Column* short; rostellum small; pollinia two, attached to a single viscidium or attached to separate viscidia, placed in a simple bursicle. *Ovary* cylindrical, subsessile or sessile, twisted, glabrous. **(JW)**

Distribution (Fig. 59.2)

A dozen species distributed in northern, central, and southern Europe, western Asia and south to North Africa. *Anacamptis collina* and *A. pyramidalis* extend east to Iran, and *A. pseudolaxiflora* extends east to Afghanistan and south to Yemen. **(JW)**

Palynology

The pollen surface of *A. pyramidalis* is hamulate, and sections show free baculae, verrucae, and granulations. Sculpturing among some species formerly included in *Orchis*, e.g. *A. coriophora*, *A. longicornu*, *A. morio*, *A. palustris*, is laevigate-scabrate, but in others (*A. laxiflora*, *A. pauciflora*, *A. sancta* R. M. Bateman, Pridgeon & M. W. Chase) is verrucose-hamulate (Schill and Pfeiffer 1977). **(AP)**

Cytogenetics

Anacamptis is characterized by diploid chromosome numbers $2n = 32, 36$. The tetraploid cytotype $2n = 4x = 72$ and the cytotypes with $2n = 54$ and $2n = 63$ have also been reported (Scrugli *et al.* 1976; Scrugli 1977; Del Prete 1978; Tanaka and Kamemoto 1980; Bianco *et al.* 1987; Capineri and Rossi 1987; Del Prete *et al.* 1991; Bianco *et al.* 1991; D'Emerico *et al.* 1993).

In *Anacamptis pyramidalis* the tetraploid cytotype comprises four copies of the basic set, indicating an autopolyploid origin. However, metaphase I in EMCs (embryo sac mother cells) usually shows 36 bivalents, with occasional quadrivalents in some cases. Cytological analyses in the triploid individuals ($2n = 3x = 54$) at metaphase I in EMC show many trivalents.

Some rare cases of triploidy ($2n = 3x = 54$) have been observed in *A. laxiflora* and *A. coriophora* subsp. *fragrans* R. M. Bateman, Pridgeon & M. W. Chase (Bianco *et al.* 1991; D'Emerico *et al.* 1993). In these specimens, meiotic plates at metaphase I in EMC have numerous trivalents, confirming the autopolyploid origin.

Careful karyological study reveals a similar 'basic karyotype' in all the *Anacamptis* species analysed (D'Emerico *et al.* 1990, 1992, 1993, 1996*b*). Apart from the pairs of chromosomes showing

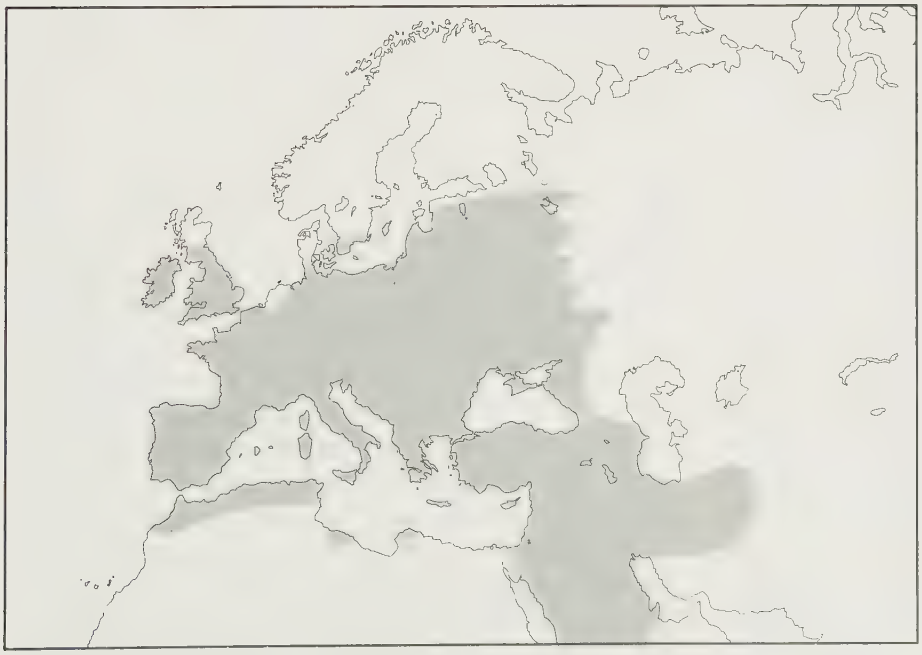

Fig. 59.2. Distribution map of *Anacamptis*.

secondary constrictions on the short arm, secondary constrictions on the long arm may also be observed together with a marker pair consisting of a secondary constriction on the short arm and a microsatellite on the long arm. In this group, *Anacamptis morio* has the most symmetrical karyotype, comprising mainly metacentric chromosomes (Fig. C.2a). There are interesting similarities to this in the karyotype of *A. longicornu*, in which metacentric chromosomes predominate over submetacentric ones. The latter is similar morphologically to *A. morio*, except for some differences in the labellum.

This parallel between karyotype and labellum morphology is observed also in *A. laxiflora* and *A. palustris*. However, *A. palustris* has a more asymmetrical karyotype. The complements of *A. laxiflora* and *A. palustris* closely resemble those of *A. morio* and *A. longicornu*, but the former pair differs in having more submetacentric chromosomes.

Karyological observation of diploid *A. pyramidalis* (Fig. C.2b) reveals a karyotype morphology similar to those of *A. morio* group. At the other extreme, *A. collina* has a more asymmetrical karyotype and possesses several chromosomes with secondary constrictions.

Karyomorphological similarities in *A. morio*, *A. longicornu*, *A. laxiflora*, *A. pyramidalis*, and *A. palustris* are confirmed by the similar reaction to differential staining technique. In none of these species is heterochromatin evident. Although the symmetry of the karyotype of *A. collina* differs with respect to that of the *A. morio* group, the chromatin of each is similar to one another (D'Emerico *et al.* 1996*b*).

Asymmetrical karyotypes characterize *A. papilionacea* and *A. coriophora*. In *A. papilionacea* the somatic chromosome complement includes a characteristic pair of chromosomes (no. 1) with two secondary constrictions, one per arm. The karyotype of *A. coriophora* includes predominantly submetacentric chromosomes.

A high variability in content and distribution of heterochromatin has been observed in *Anacamptis*. The methods of C-banding and fluorescent H33258 staining allow the identification of constitutive heterochromatin only in *A. papilionacea* and *A. coriophora*. *Anacamptis papilionacea* possesses a total of four C-bands per haploid karyotype on the chromosomes no. 1, 2, and 6. All chromosomes have centromeric heterochromatin (Fig. C.4a). Some differences in heterochromatin position have been observed in specimens of *A. papilionacea* subsp. *grandiflora*, in which Giemsa C-banding confirmed heterochromatin distribution only on chromosome pair no. 1. In this case, differences presumably arise from some degree of isolation by ecological barriers with natural selection favouring different genotypes in different areas.

A comparison of karyotype asymmetry indices, heterochromatin content, and distribution reveals that only the taxa with more asymmetrical karyotypes possess appreciable amounts of heterochromatin. For example, *A. coriophora* consistently exhibits a large amount of telomerically distributed heterochromatin (D'Emerico *et al.* 1996b; Fig. C.4b), whether the plants studied are from Spain or Italy.

The natural interspecific hybrid, *A. morio* × *papilionacea*, appears to be a chromosome structural hybrid. The diploid complement of *A. morio* is 36, and *A. papilionacea* has 32 chromosomes; the hybrid has 34 chromosomes. Meiotic plates in hybrid specimens at metaphase I in EMC show mostly univalents and few bivalents, whereas both parent species exclusively exhibit bivalents. With C-banding, two chromosomes are characterized by presence of large telomeric heterochromatic blocks on the short arms, which strongly resemble the ones observed in *A. papilionacea* (D'Emerico *et al.* 1996*a*). In one population two hybrid specimens were triploid, with 52 chromosomes (18 bivalents and 16 univalents) at metaphase I in EMC. Another case of allotriploidy occurs in a new interspecific hybrid, *Anacamptis collina* × *morio*, with $2n = 54$.

In preliminary analysis of some *Anacamptis* species, fluorescent *in situ* hybridization has been used to identify DNA sequences on chromosomes and physical location of sites of highly repeated genes. The DNA probes utilized are pTa71, which localizes repeated sequences of 18S–5.8S–26S, and pTa794, which localizes 5S genes of ribosomal DNA. Using the probe pTa71 in *A. papilionacea*, rDNA genes have been identified on one chromosome pair; with pTa794, rDNA genes have been identified on two pairs (Galasso *et al.*, unpublished). **(SD)**

Phytochemistry

Infection of the tubers of either *A. latifolia* (cited as *Orchis latifolia*), *A. morio* (cited as *O. morio*) or *A. pyramidalis* with a strain of *Rhizoctonia repens* from *Orchis militaris* results in the synthesis of the phytoalexin orchinol (2,4-dimethoxy-7-hydroxy-9,10-dihydrophenanthrene) and *p*-hydroxybenzylalcohol. In the case of *A. coriophora* (= *O. coriophora*) only *p*-hydroxybenzylalcohol was detected under the same conditions. These observations were made as part of a survey of orchinol and *p*-hydroxybenzylalcohol production in a number of species representing genera in subtribe Orchidinae (Nüesch 1963; Gaumann *et al.* 1960).

The leaves of *A. papilionacea* (cited as *Orchis papilionacea*) contain quercetin. This flavonol aglycone was detected in acid-hydrolysed extracts of leaf tissue, indicating that it arises from quercetin *O*-glycosides (C. A. Williams 1979).

Baytop and Sezik (1968) reported on the chemical analysis of tubers of *A. morio* (cited as *Orchis morio*), *A. sancta* (cited as *Orchis sancta*), and *A. pyramidalis* collected in south-west Anatolia, Turkey. Their results were summarized in a later review by Ernst and Rodriguez (1984). Dried tubers are marketed as 'salep', the quality of which depends on the mucilage content. In a survey of salep from the tubers of species collected in this region, it was concluded that the best grades for pharmaceutical use should contain more than 40% mucilage and less than 5% ash (Sezik 1967). Aqueous extraction of young tubers of *A. morio* gave a polysaccharide characterized as a glucomannan with D-glucopyranosyl and D-mannopyranosyl residues in the approximate ratio of 1.0:3.3, respectively (Buchala *et al.* 1974). The polysaccharide backbone comprises β (1 $\rightarrow$ 4)-linked glucopyranosyl and mannopyranosyl residues with approximately seven branch points per molecule, thought to be at C-3 of the hexose units. The acetyl content of the polysaccharide was estimated to be 5.3%, with the sites of acetylation restricted to C-2 and C-3 of the mannopyranosyl units. **(NV, RG)**

Ecology

Members of the European genus *Anacamptis* are terrestrial orchids many of which typically grow on shallow, well-drained, calcareous soils such as chalk and limestone. These include the Mediterranean species, *A. boryi*, *A. collina*, *A. papilionacea*, *A. sancta*, and the more widespread species *A. pyramidalis* which, in Britain, is a characteristic orchid of the chalk downlands in southern England and also calcareous sand dunes (Summerhayes 1951; Davies *et al.* 1988; Delforge 1995; Rasmussen 1995). *Anacamptis morio* has the widest ecological range of the group (Summerhayes 1951; Delforge 1995). Although it prefers calcareous soils, it often grows on neutral to slightly acid substrates. In parts of Britain it flourishes in sand dune slacks (Lang 1989), and it is particularly common on heavy marl and clay soils if they are not too wet (Summerhayes 1951; Sanford 1991; Wells *et al.* 1998). In contrast, *A. laxiflora* and *A. coriphora*, which tend to grow on slightly acid to alkaline soils, are more often found where the soils are permanently wet, such as in bogs, marshes, seepage zones, and other areas prone to flooding (Davies *et al.* 1988; Delforge 1995).

Anacamptis grows at a range of elevations throughout its distribution. *Anacamptis sancta*, for example, often occurs near the coast and always below 900 m, whereas *A. pyramidalis* and *A. coriophora* can grow at elevations over 2000 m (Davies *et al.* 1988; Delforge 1995). Members of the genus grow in a variety of grassland habitats including dry, nutrient poor pastures and meadows, old established dunes, marshy moorland, roadside verges and railway embankments, as well as in open shrub and woodland such as maquis, open pine woods, and olive groves in the Mediterranean region (Pettersson 1976; Davies *et al.* 1988; Delforge 1995). The variety of habitats within which individual *Anacamptis* species are able to grow depends on their level of shade tolerance. *Anacamptis morio*, for example, normally only occurs in open habitats in full sunlight. Thus, in Britain it typically grows in species-rich grasslands such as old hay meadows (i.e. *Cynosurus cristatus-Centaurea nigra* grassland, MG5, in Rodwell's National Vegetation Classification, 1992) and in pastures where the turf is short and may be grazed. In these habitats, *A. morio* is often associated with cowslips (*Primula veris* Mill.; Primulaceae) and other species characteristic of undisturbed grassland such as adder's tongue (*Ophioglossum vulgatum* L.; Ophioglossaceae) (Summerhayes 1951; Lang 1989; Sanford 1991). Summerhayes (1951) noted that where the vegetation is taller *A. morio* is absent and that it rarely occurs in shaded habitats such as woodlands. *Anacamptis pyramidalis* is more shade-tolerant. In Britain it is a component of the *Hieracium* sub-community of *Bromus-Brachypodium* grassland, CG5 (Rodwell 1992). The sward of its typical chalk grassland habitat in southern England is composed of relatively tall grasses. *Anacamptis pyramidalis* also grows among marram grass (*Ammophila arenaria* Link) and lyme grass (*Elymus* spp.) on sand dunes (Lang 1989; Allan *et al.* 1993), but it is less common in short grassland where other orchid calcicoles are often found (Summerhayes 1951). It can withstand partial shade since it sometimes occurs among low shrub of hawthorn and blackthorn or in some beech, oak, and other woodlands where their canopies are relatively open (Summerhayes 1951; Davies *et al.* 1988). Other members of the genus that occur in open woodlands or shrubland in the Mediterranean include *A. champagneuxii*, *A. sancta*, *A. collina*, *A. papilionacea*, and *A. boryi* (Davies *et al.* 1988; Delforge 1995).

The peak flowering period of *Anacamptis* is from March to June, although this varies between species due to the elevation and latitude of individual populations. The Mediterranean species, *A. collina*, is early flowering, commencing in December in some localities and with successive cohorts coming into flower until April (Delforge 1995). In contrast, *A. sancta* and *A. coriophora*, also growing in the Mediterranean, flower later, with anthesis taking place between April and July (Davies *et al.* 1988; Delforge 1995). In the south of its range in the Algarve in Portugal, *Anacamptis morio* flowers in March, several weeks earlier than the same species in the north of its range in Scotland where it flowers in May (Neiland 1994). The widespread species *A. pyramidalis* flowers early in the summer across western Europe, e.g. from mid-June until the end of July in Britain, which is several weeks later than many other orchids growing in the same habitat in England (Lang 1989). This characteristic of flowering some time after co-occurring orchid species is also noted for the eastern Mediterranean species, *A. sancta*, which flowers in April (Davies *et al.* 1988).

Anacamptis orchids are usually 'winter-green' species. Normally each plant produces a rosette of leaves in the autumn that remains green and functional throughout the winter and spring and senesces early, often during the flowering period. Following fruit-set, the orchids perennate as underground tubers. This is of adaptive advantage for growth in a Mediterranean climate where *Anacamptis* is thus able to survive the summer drought. The tubers are replaced annually, and under favourable conditions more than one tuber may develop from the buds at the base of the aerial stem. Formation of extra daughter tubers from the mother plant is the means by which vegetative propagation can be achieved in this and other terrestrial genera such as *Dactylorhiza* (Rasmussen 1995).

Fruit formation in *Anacamptis* species is normally quite low. Average fruit-set figures of 21.1%, 29.0%, and 33.5% have been recorded from *A. morio*, *A. collina*, and *A. pyramidalis* populations in Europe (Neiland and Wilcock 1998). A higher proportion of flowers of *A. papilionacea* examined by Vogel (1972) in Germany set fruit (50%), but this population was unusual in that it was pollinated during regular patrolling flights of territorial bees. Average seed set per capsule varies among species in the genus. Salisbury (1942) counted about 2000 seeds in a single capsule of *A. pyramidalis* and estimated that the average output of seeds from an individual plant could be 35 000 seeds. The number of seeds formed per capsule of *A. morio* ranges from 2000 to 4000, and seed outputs per plant of between 20 000 and 32 000 seeds have been calculated using field observations of average numbers of capsules per plant of *A. morio* (Salisbury 1942; Neiland 1994).

Germination of *Anacamptis* seeds normally takes place in the spring after which a protocorm is formed. In some species, e.g. *A. morio* and *A. papilionacea*, this rapidly develops and produces its first root in the autumn and the first foliage leaf in the following winter or spring after which time a tuber develops at the base of the stem. Growth of the protocorm is slower in *A. pyramidalis*, and it may take 1–3 years before the first tuber and foliage leaves appear, depending on growth conditions at field sites (Rasmussen 1995). The formation of the inflorescence is delayed still further. Wells (1981) stated that flowering first takes place four to five years after germination in *A. morio* and seven to eight years after germination in *A. pyramidalis*. The protocorm and rhizome of *Anacamptis* species are highly mycotrophic, but the endophytes involved have yet to be identified (Rasmussen 1995). Seeds of some species have been germinated symbiotically with fungal strains, including seeds of *A. laxiflora* with *Ceratobasidium corrigerum* (Muir 1987, 1989), *A. papilionacea* with *Epulorhiza* sp. (Andersen 1990, cited in Rasmussen 1995), and *A. morio* with a *Ceratobasidium*-like isolate obtained from the Royal Botanic Gardens, Kew (McKendrick 1996*a*). It is now possible to propagate a variety of *Anacamptis* species asymbiotically on a range of nutrient media (e.g. Malmgren 1993). The time to reach maturity may be quite short; Frosch (1980) reported that *A. morio* plants initially cultured by asymbiotic methods reached flowering within 23 months. Symbiotic techniques have been successfully used at Kew to provide seedlings of several *Anacamptis* species (including *A. laxiflora* and *A. morio*) for re-introduction to field sites (Muir 1989) as a means of conserving these species, the numbers of which have been declining in England in recent years.

Some members of the genus are abundant locally, and under favourable conditions large populations of flowering plants may be formed (Summerhayes 1951) that can be long-lived. *Anacamptis pyramidalis*, for example, is known to have persisted in high numbers for over 100 years at one locality on the east coast of Scotland (Allan *et al.* 1993) and at another site in Kent in southern England (Lang 1989).

As with many congeneric orchids, *A. pyramidalis* is able to colonize new localities rapidly by means of seed dispersal. For example, Nothdurft (1995) described the appearance, presumably due to wind dispersal, of a flowering plant of *A. pyramidalis* in a garden in Germany 40 km from the nearest population. *Anacamptis laxiflora* in the Mediterranean is also a typical weedy species and quickly invades abandoned fields (Pettersson 1976). Populations of *Anacamptis* species have been described as fluctuating in numbers from year to year. *Anacamptis morio*, for example, is thought to be short-lived and monocarpic (Summerhayes 1951). However, in a recent long-term demographic study by Wells and his co-workers it has been shown that, after reaching a critical size, *A. morio* plants can flower for several years in succession (for example up to 17 out of the 18 years of the study in a few cases). In this population, a large proportion of plants flowered each year (usually >40%). The probability of an individual flowering increases with leaf number, but there seems to be no clear relationship between flowering and climatic factors, which could explain variations in the flowering performance of the population from year to year (Wells *et al.* 1998).

In addition to the more common and widespread species, *Anacamptis* includes some species with localized distributions, e.g. the eastern Mediterranean species, *A. sancta*, *A. coriophora*, and the southern Greek endemic *A. boryi* (Delforge 1995). Many of these localized species are also declining in numbers. *Anacamptis morio* in Britain was cited as one of the commonest of British orchids by Summerhayes (1951), but within three decades it had undergone a dramatic decline and is now considered to be a threatened species (Lang 1989). The major reason for the disappearance of *Anacamptis* species has been alteration of their grassland habitat. Seedlings can be physiologically tolerant of some shade (e.g. *A. morio*, McKendrick 1996*b*), but in the field the plants can readily become shaded-out if taller plants become dominant in the habitat. For example, on the Swedish island of Öland, Lind (1992) showed that populations of *A. pyramidalis* growing at sites that were not kept open by grazing were decreasing because of the invasion of taller grasses and shrubs. Changes in the vegetation composition due to re-seeding old pastures, drainage or fertilization can also have a detrimental effect on *Anacamptis* populations (Sanford 1991; McKendrick 1996). Agricultural improvement of ancient herb-rich meadows by the application of fertilizer has been used to explain the recent dramatic decline of *A. morio* in England. High levels of inorganic phosphorus can be toxic to the orchids; even low levels may improve hay yield but lead to the demise of the orchid, which suffers increased competition from the surrounding plants (Silvertown *et al.* 1994; McKendrick 1996*a*). **(RN)**

Pollination

The newly circumscribed genus *Anacamptis* (Bateman *et al.* 1997) comprises species that differ strongly in floral characters and pollination. Most of these species do not provide nectar in their spurs. The pollination biology of *Anacamptis pyramidalis* was investigated by Darwin (1888). He observed 23 species of day- and night-flying Lepidoptera visiting the plants. Nazarov and Yefetov (1994) confirmed Darwin's observations that Lepidoptera, especially Zygaenidae, are the most important pollinators. Pollinators are attracted to the flowers, although they are not rewarded. Nazarov and Yefetov (1994) therefore suggested that pollinators are attracted because the inflorescences of *A. pyramidalis* are similar to those of food plants. *Anacamptis morio*, which was studied in detail in Scandinavia (Nilsson 1984), displays a similar pollination strategy. The species exploits mainly naive bumble-bee queens, which visit the showy flowers while searching for nectar after hibernation. The morphology of the spur (i.e. width of spur entrance and spur length) seems not ideally suited for these large and relatively long-tongued pollinators, and solitary bees may be more efficient when present. A different pollination system may be acting in *A. papilionacea*. Vogel (1972) observed males of the solitary bee *Eucera tuberculata* using this species as flight posts while searching for females. Dafni (1987) considered these plants therefore as rendezvous flowers (Faegri and van der Pijl 1966). In contrast to these nectarless species, *A. coriophora* does provide nectar in its short spur (Dafni and Ivri 1979; Eberle 1974; Peisl and Forster 1975; Vöth 1975) and is pollinated by a wide variety of insects. The pollination strategy of *A. pyramidalis* and *A. morio*, food deception, has also been reported for *A. collina*. In contrast to most other food-deceptive taxa, however, Dafni and Ivri (1979) suggested that *A. collina* mimics the closely related, nectariferous *A. coriophora*. *Anacamptis collina* is pollinated by the same insect species that also visit the model. Different placement of pollinaria on the pollinators reduces the probability of hybridization between both species. This pollination strategy, in which a non-rewarding species mimics a rewarding plant, is known as Batesian floral mimicry (Dafni 1984; Dafni 1987; Dafni and Ivri 1981; Johnson 1994; Roy and Widmer 1999). Strong evidence for the existence of floral Batesian mimicry was also found in *A. israelitica* (H. Baumann & Dafni) R. M. Bateman, Pridgeon & M. W. Chase (Dafni and Ivri 1981) which mimics the *Bellevalia flexuosa* Boiss. (Hyacinthaceae) seed set in *A. israelitica* is higher in the presence of the model, as expected under Batesian floral mimicry (Dafni and Ivri 1981). **(AW, SC, AD)**

Uses

None recorded other than horticultural. **(JW)**

Cultivation

Species occur in open grassland over lime or chalk. They will grow well in containers in compost C (with added dolomite) and can be naturalized in short turf. **(CB)**

Taxonomic notes

Formerly monospecific, *Anacamptis* has been expanded to include all species of *Orchis sensu lato* that possess $2n = 32$ or 36 chromosomes (Bateman *et al.* 1997). It now includes *Orchis collina* and the *O. coriophora*, *O. laxiflora*, *O. morio*, and *O. papilionacea* complexes. *Anacamptis pyramidalis* is distinctive in its floral morphology, probably the result of adaptations reflecting a switch to lepidopteran pollinators. The other members of this newly defined genus are difficult to distinguish morphologically from *Orchis sensu stricto*, but their flowering stems bear cauline sheathing leaves that are absent in the latter; the leaves are never spotted, and the dorsal sepal and petals usually form a hood over the column. **(JW)**

Taxonomic literature

Bateman, R. M., Pridgeon, A. M., and Chase, M. W. (1997). Phylogenetics of subtribe Orchidinae (Orchidoideae, Orchidaceae) based on nuclear ITS sequences. 2. Infrageneric relationships and reclassification to achieve monophyly of *Orchis sensu stricto*. *Lindleyana*, **12**, 113–41.

60. ANDROCORYS

Androcorys Schltr., *Orch. Sino-Jap. Prodr.*, **52** (1919). Type species: *A. ophioglossoides* Schltr.

Derivation of name

From the Greek *andros*, male, and *korys*, helmet, in allusion to the hood formed by the dorsal sepal and petals. **(PC)**

Description (Plate 80; Fig. 60.1)

Small, glabrous, terrestrial *herbs* growing from globose, hairy tubers. *Leaves* 1–2, suberect, ovate, green. *Inflorescence* erect, densely few–many-flowered, spicate; bracts small, green, glabrous. *Flowers* small, green. *Dorsal sepal* ovate, concave forming a hood with the petals over the column. *Lateral sepals* free to somewhat connate, spreading, similar to the dorsal sepal. *Petals* entire, ovate to orbicular, smaller than the sepals. *Labellum* deflexed, entire, ovate to ligulate, obscurely saccate to concave at the base, ecallose. *Column* short, erect; anther bilocular; connective broad; pollinia clavate, sessile; viscidia two; stigma pulvinate, bigibbose; rostellum triangular, erect; lateral appendages two. *Ovary* sessile, slightly twisted. **(PC)**

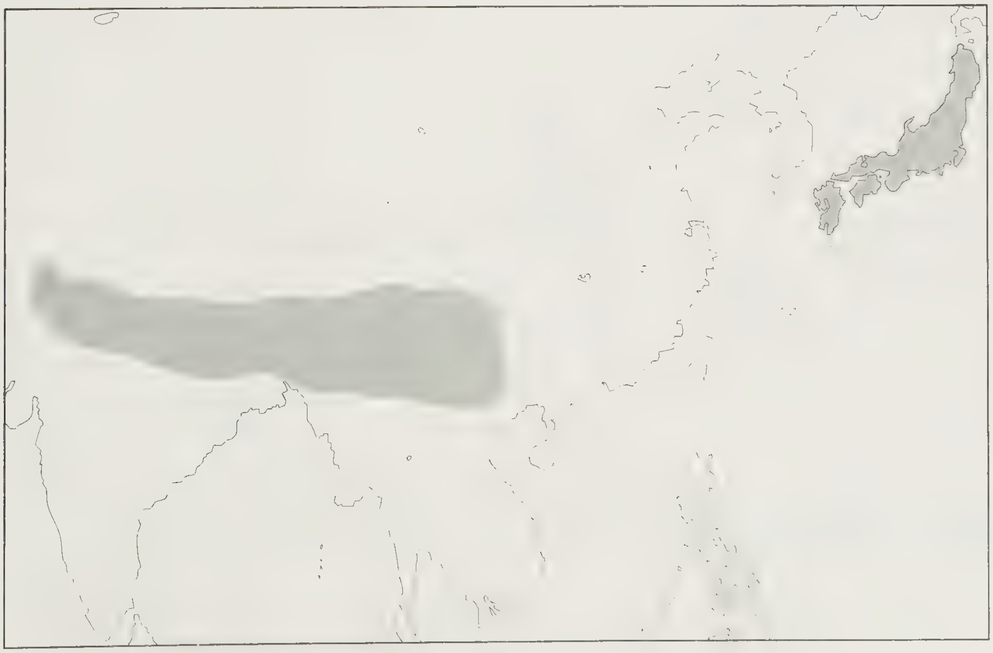

Fig. 60.2. Distribution map of *Androcorys*.

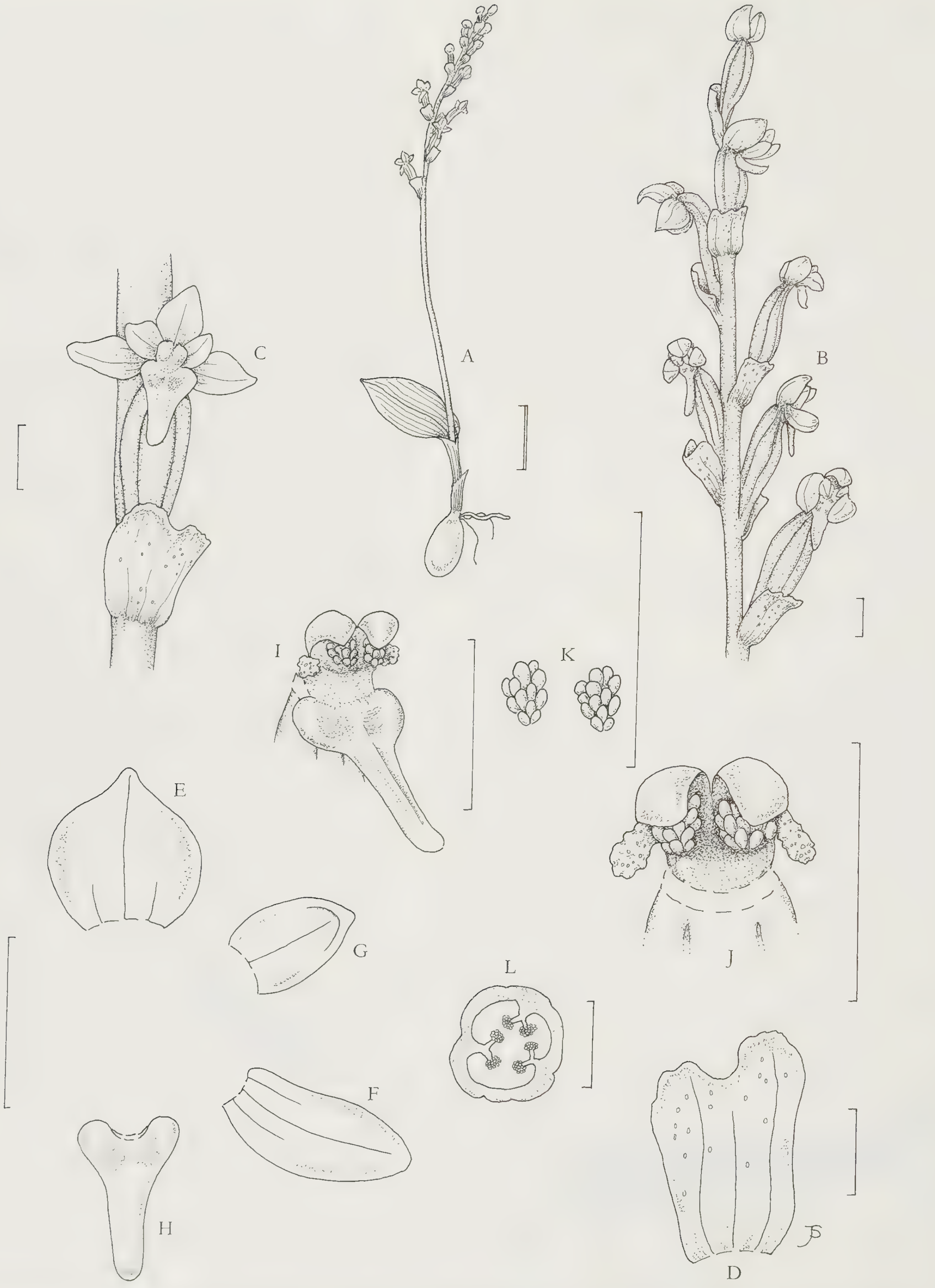

Fig. 60.1. *Androcorys gracilis* Schltr. A. Habit; B. Inflorescence; C. Flower; D. Bract; E. Dorsal sepal; F. Lateral sepal; G. Petal; H. Labellum; I. Labellum and column, oblique view; J. Column, front view; K. Pollinia; L. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Gamble 9570.*

Distribution (Fig. 60.2)

A small genus of about ten species ranging from Kashmir in the Himalayas across to China, including Taiwan, and with two species in Japan. **(PC)**

Ecology

Androcorys species grow in short grassland, the majority in the Himalayas and Chinese mountains at elevations up to 5500 m, probably the highest elevations at which orchids grow. The rare Japanese species, *A. japonensis* Maek., which is found in Yatsugatake on Honshu, flowers in August (Ohwi 1965). **(PC, RN)**

Cultivation

Terrestrials mainly, with occasional lithophytes, from India to east Asia, mainly at higher elevations. Compost B, C, or D depending upon habitat. **(CB)**

Taxonomic notes

Androcorys is closely allied to *Herminium* but lacks a lobed lip. The relationship between these genera needs further investigation; several Chinese species currently treated in *Herminium* may fit better in *Androcorys*, particularly those with a spurred lip. **(PC)**

61. BARLIA

Barlia Parl., *Nouv. Gen. Piant. Monocot.*, **5** (1858). Type species: *Barlia robertiana* (Loisel.) Greuter.

Derivation of name

Named by Filippo Parlatore (1816–1877) in honour of his friend and botanist, Joseph H. J. B. Barla. **(JW)**

Description (Plate 81; Fig. 61.1)

Robust *herbs*. *Rootstock* tuberous, tubers large, entire. *Stem* erect, thick, leafy below, glabrous. Basal *leaves* large, broad, shiny, unspotted, cauline leaves grading into amplexicaul bracts. *Inflorescence* cylindrical, densely many flowered; floral bracts membranous. *Flowers* large, showy, olive-green to purple-violet. *Dorsal sepal* and *petals* loosely connivent to form a hood, lateral sepals spreading, glabrous. *Labellum* shortly spurred, deeply three lobed, with two parallel median ridges running from spur entrance to middle of mid-lobe, side lobes falcate, undulate, mid-lobe bilobed, spur conical, saccate, with a globular, papillose to hairy internal nectary. *Column* broad; rostellum lamellate; stigmatic cavity elongate, ± cordate; lateral appendages prominent; pollinia two, attached by a moderately thick caudicle to a single viscidium enclosed in a bursicle. *Ovary* cylindrical, subsessile, glabrous. **(JW)**

Distribution (Fig. 61.2)

A genus of two species only. *Barlia metlesicsiana* Teschner is endemic to the Canary Islands (Tenerife). *Barlia robertiana* is widespread from Portugal, Spain, and across the Mediterranean region, east to southern Turkey and south to North Africa. **(JW)**

Palynology

Sculpturing of *B. robertiana* is laevigate-scabrate, said to be comparable to *A. morio* (as *O. morio*; Schill and Pfeiffer 1977), which accords well with cytological and molecular evidence. **(AP)**

Cytogenetics

The only species of the genus *Barlia* studied, *B. robertiana*, has a diploid chromosome number of $2n = 36$. There is general similarity among the karyotypes of *Anacamptis*, *Himantoglossum*, and *Barlia*. The complement of *B. robertiana* is characterized by mainly metacentric chromosomes and low asymmetrical karyotype (D'Emerico *et al.* 1992). As for the *A. morio* group, no heterochromatin is evident. **(SD)**

Phytochemistry

Infection of the tubers of *B. robertiana* (cited as *Himantoglossum longibracteatum*) with a strain of *Rhizoctonia repens* from *Orchis militaris* results in the synthesis of the phytoalexin orchinol (2,4-dimethoxy-7-hydroxy-9,10-dihydrophenanthrene) and *p*-hydroxybenzylalcohol. These observations were made as part of a survey of orchinol and *p*-hydroxybenzylalcohol production in a number of species representing genera in subtribe Orchidinae (Nüesch 1963; Gaumann *et al.* 1960).

A preliminary examination of the anthocyanin content of *B. robertiana* flowers indicated that they contain cyanidin 3-glucoside (chrysanthemin), cyanidin 3,5-diglucoside (cyanin), and the pigments orchicyanin I and II (Uphoff 1979). Strack *et al.* (1989) also found cyanidin 3,7-diglucoside (seranin), ophrysanin, and serapianin in a later survey of this species and recorded a similar anthocyanin profile in *B. metlesicsiana*. Orchicyanins I and II, ophrysanin, and serapianin were identified as cyanidin glucosides acylated with oxalic acid (Strack *et al.* 1986, 1989).

Baytop and Sezik (1968) reported on the chemical analysis of tubers of *B. robertiana* collected in south-west Anatolia, Turkey. Their results were summarized in a later review by Ernst and Rodriguez (1984). See *Anacamptis*. **(NV, RG)**

Ecology

Barlia normally grows on neutral to alkaline soils, often on nutrient-poor and free-draining chalk soils (Davies *et al.* 1988). Typical habitats in which members of the genus grow include open grassland, scrubland with pine, and woodland clearings, and in suitable habitats they can grow at high elevations above sea level, e.g. at 1000 m on the island of Tenerife (Leon-Aren *et al.* 1992). *Barlia* species are some of the earliest orchids to flower in the Mediterranean region, e.g. in north Africa *B. robertiana* blooms in December. Elsewhere in the region, the peak flowering time is February to March, but it is slightly later at higher elevations. Perennation is by means of 2–3 large, ovoid underground tubers. *Barlia* is more common in the western Mediterranean than elsewhere in its range (Davies *et al.* 1988). **(RN)**

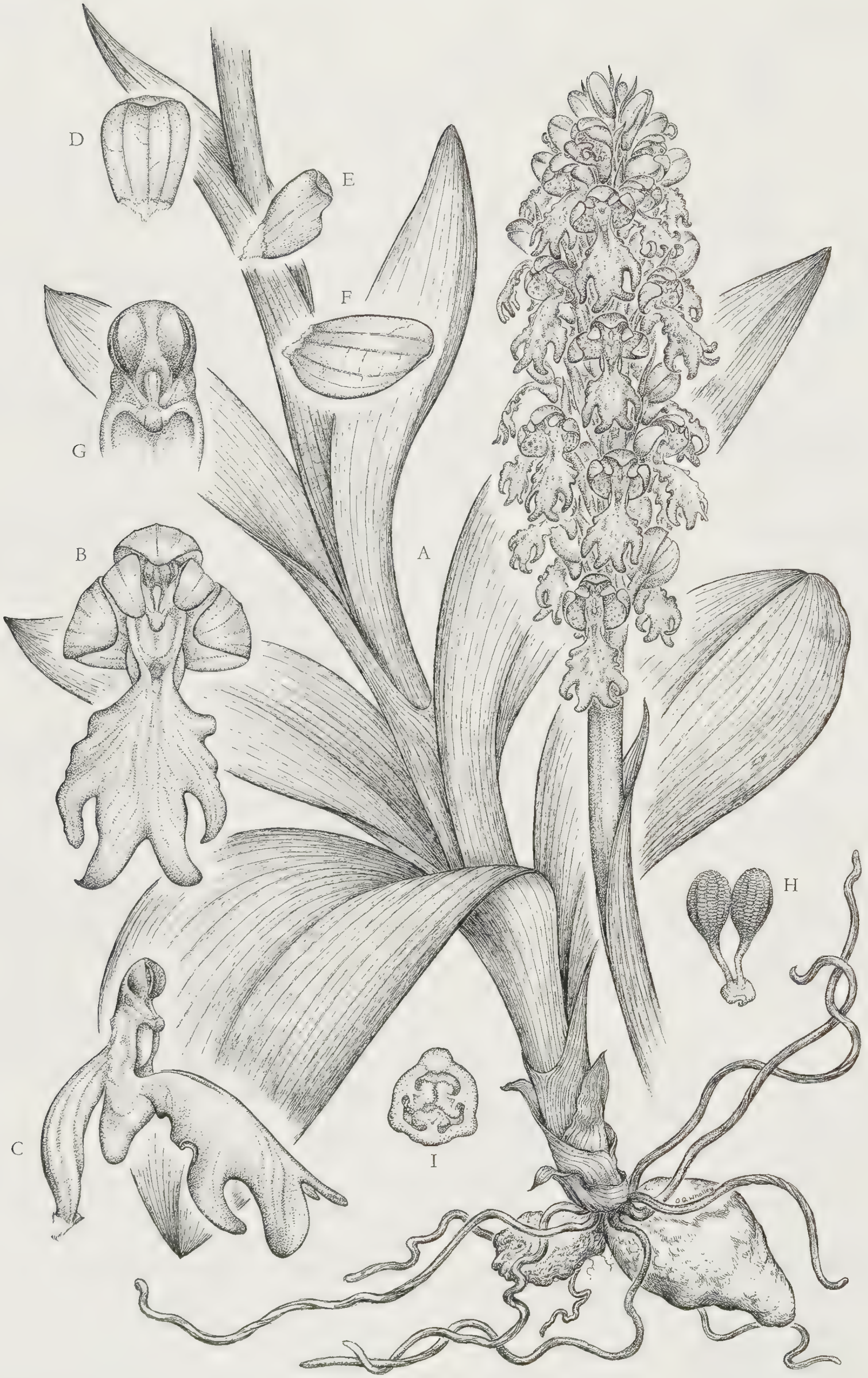

Fig. 61.1. *Barlia robertiana* (Loisel.) Greuter. A. Habit, ×1; B. Flower from front, ×3; C. Flower, oblique view, perianth removed, ×3; D. Dorsal sepal, ×3; E. Petal, ×3; F. Lateral sepal, ×3; G. Column apex, ×6; H. Pollinarium, ×6; I. Ovary, transverse section, ×6. Drawn by Oliver Q. Whalley from Kew Spirit Collection nos. 43456 and 19442.

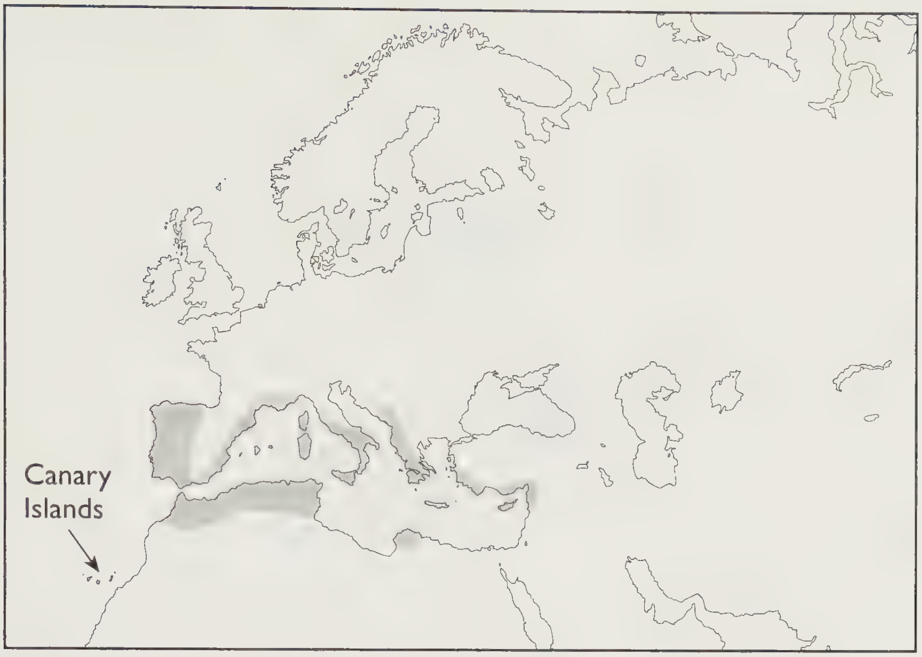

Fig. 61.2. Distribution map of *Barlia.*

Pollination

The presence of nectar in the short spur of *Barlia* is disputed. Both species, the widespread *B. robertiana* and *B. metslesicsiana* W. P. Teschner (endemic to the Canary Islands), however, are pollinated by bees (van der Cingel 1995 and references therein). **(AW, SC, AD)**

Uses

Tubers are collected for salep production, especially in Turkey (see *Anacamptis*). **(PC)**

Cultivation

Barlia occurs in open grassland and scrub over lime or chalk. Plants grow well in containers in compost C with added lime. **(CB)**

Taxonomic literature

Nelson, E. (1968). *Monographie und Ikonographie der Orchidaceen Gattungen* Serapias, Aceras, Loroglossum, Barlia: 52–62. E. Nelson, Chernex-Montreux.

Sunderman, H. and Taubenheim, G. (1982). Die Verbreitung der Orchideen in der Türkei II/2. Ein Beitrag zur 'Flora of Turkey' 3, 5, 6. Die Gattungen *Anacamptis*, *Barlia* und *Aceras*. *Orchidee*, **33**, 222–7.

62. BARTHOLINA

Bartholina R.Br. in Aiton, *Hort. Kew.*, ed. 2, **5**, 194 (1813). Type species: *B. pectinata* (Thunb.) R.Br.

Derivation of name

Commemorating Thomas Bartholin, the Danish anatomist and physiologist. **(JW)**

Description (Plate 82; Fig. 62.1)

Dwarf, terrestrial *herbs* growing from ovoid-oblong tubers. *Leaf* solitary, prostrate, fleshy, reniform-orbicular, amplexicaul, hairy. *Inflorescence* one-flowered; scape hairy, lacking sterile bracts; bract lanceolate, much shorter than the the ovary, hairy or glabrous. *Flower* large for plants, resupinate, spidery; pedicel and ovary curved, hairy or glabrous. *Sepals* subsimilar, free, erect, green, hairy or glabrous. *Petals* erect, falcate or sinuous, lanceolate, adnate to the dorsal sepal, white or green, glabrous. *Labellum* much larger than the sepals and petals, spreading-deflexed, three-lobed, glabrous, spurred at the base, white with white or green lacerae; lobes deeply lacerate, tapering or clavate at the tips of each division; spur short, shorter than the ovary, tapering-conical. *Column* erect; anther loculi subparallel, connivent toward apex, the connective not distinct; pollinia two, clavate with elongated caudicles, coarsely granular; viscidia two, small, reniform; rostellum three-lobed, the mid-lobe short, reflexed, the side lobes sessile; stigma sessile. **(JW)**

Distribution (Fig. 62.2)

A small genus of two species in Cape Province of South Africa. **(JW)**

Ecology

Orchids belonging to the South African endemic genus *Bartholina* are terrestrial species, for which the distribution extends from the south-western and southern Cape Province to the semi-arid Namqualand to the southern borders of the Great Karoo. The most common species is *B. burmanniana*, which can form extensive colonies on pebbly ground on the veld. *Bartholina etheliae* is much rarer, and normally only small colonies or individual plants are found growing under shrubby vegetation. It flowers from October to January after a period of summer dormancy during the dry period, the aerial stem arising from the small, spherical tuber

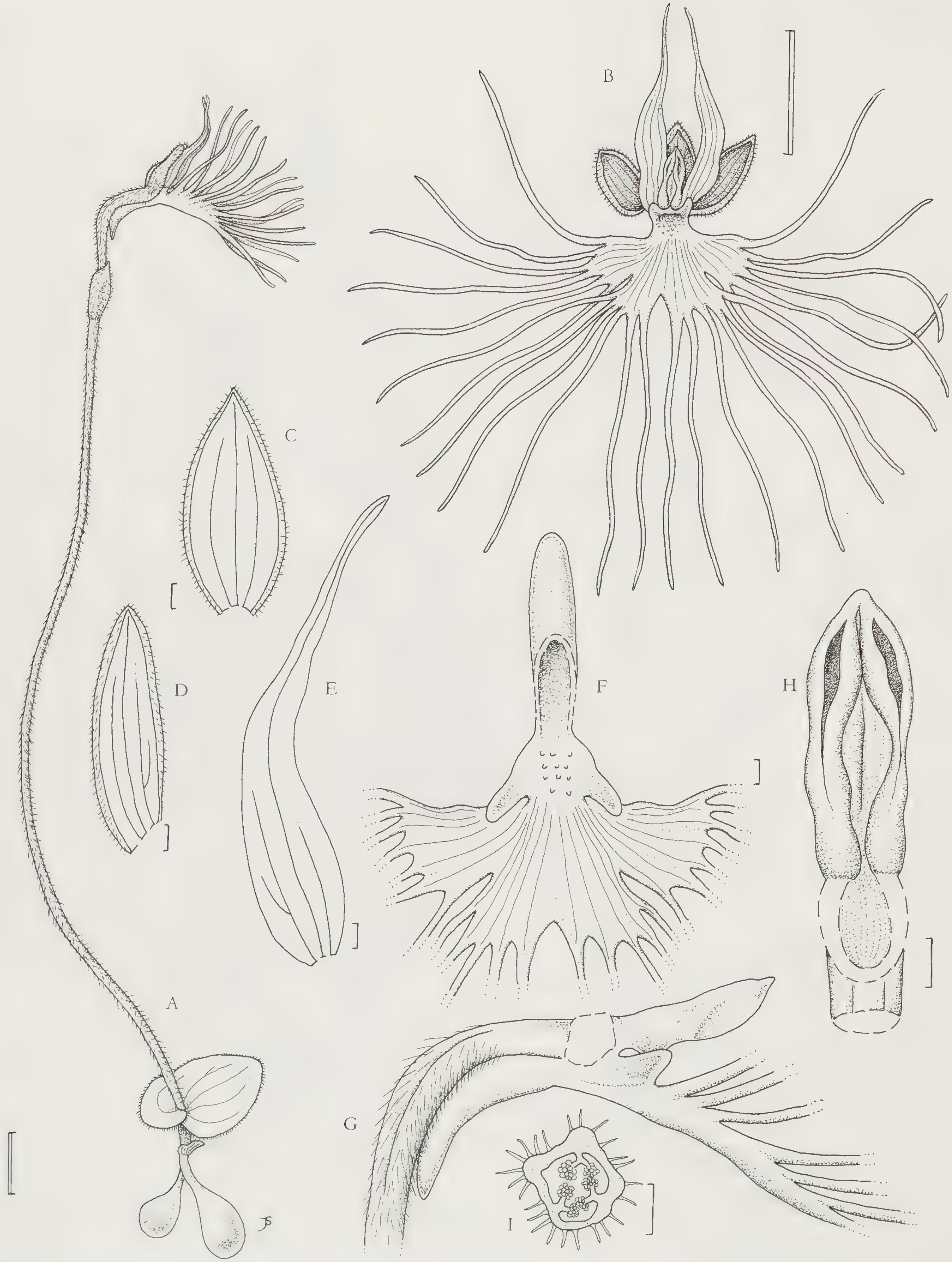

Fig. 62.1. *Bartholina burmanniana* Ker-Gawl. A. Habit; B. Flower, front view; C. Dorsal sepal; D. Lateral sepal; E. Petal; F. Labellum; G. Labellum and column, side view; H. Column, front view; I. Ovary, transection. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Wordsell 52* and Kew Spirit Collection no. 27855.

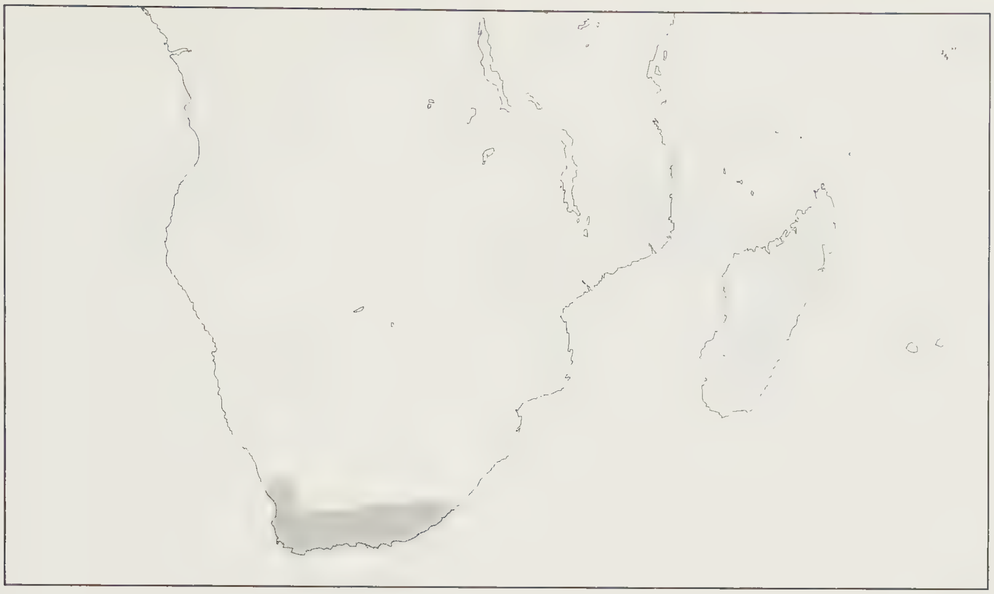

Fig. 62.2. Distribution map of *Bartholina.*

underground prior to anthesis. The flowering period of *B. burmanniana* is earlier, between August and November, depending on the aspect of the habitat. In this species, the occurrence of flowering is promoted by fires on the veld (Schelpe 1966). **(RN)**

Uses

None recorded. **(JW)**

Cultivation

These plants require dry dormancy, sandy compost, and good drainage. Composts C or E. **(CB)**

Taxonomic notes

Bartholina is closely allied to *Holothrix* but is distinguished by a solitary large flower with petals that are not dilated and divided at the apex. The merit of separating it from *Holothrix* needs further investigation. The most recent account of the genus is given by Stewart *et al.* (1982). **(JW)**

Taxonomic literature

Stewart, J., Linder, H. P., Schelpe, E. A., and Hall, A. V. (1982). *Wild Orchids of South Africa.* Macmillan South Africa, Johannesburg.

63. BENTHAMIA

Benthamia A. Rich., *Mem. Soc. Hist. Nat. Paris*, **4**, 37 (1828), *non* Lindl. (1833). Type species: *Benthamia latifolia* A. Rich. (lectotype selected here).

Rolfeella Schltr., *Repert. Spec. Nov. Regni Veg. Beih.*, **33**, 18 (1924). Type species: *R. glaberrima* (Ridl.) Schltr. (= *Benthamia glaberrima* (Ridl.) H.Perrier).

Derivation of name

Commemorating George Bentham, the English botanist and co-author with Sir Joseph Hooker of the three-volume *Genera Plantarum* (1800–1884). **(PC)**

Description (Plate 83; Fig. 63.1)

Terrestrial or less commonly epiphytic glabrous *herbs* with 2–7 swollen elongate roots. *Stems* erect, leafy in lower part. *Leaves* 1—several, basal or radical, lanceolate, ovate or elliptic, if radical then sheathing at base. *Inflorescence* erect, few- to densely many-flowered; bracts small, usually as long as or longer than the flowers. *Flowers* small, whitish, green or yellow, resupinate. *Sepals* and *petals* subsimilar, free, entire, not spreading widely. *Labellum* larger than the sepals and petals, sometimes entire, more often trilobed, lacking a callus; spur short, cylindrical or scrotiform, entire or bilobed at apex. *Column* short, erect; anther bilocular, locules parallel; pollinia two, granular, lacking caudicles, viscidia two, flat, ovate or subelliptic; rostellum small, tridentate or trilobed; stigma lobes short, convex. **(PC)**

Distribution (Fig 63.2)

A genus of about 25 species endemic to Madagascar and the Mascarenes. **(PC)**

Ecology

Benthamia species are terrestrial orchids in cool forest, deep shade on the forest floor, woodlands, montane grassland, grassland, seasonal marshes and ericaceous scrub, and on granite outcrops; sea level to 2600 m. A few species can be epiphytic. They flower between August and October (D. L. Roberts, personal communication). **(PC, RN)**

Uses

None recorded. **(PC)**

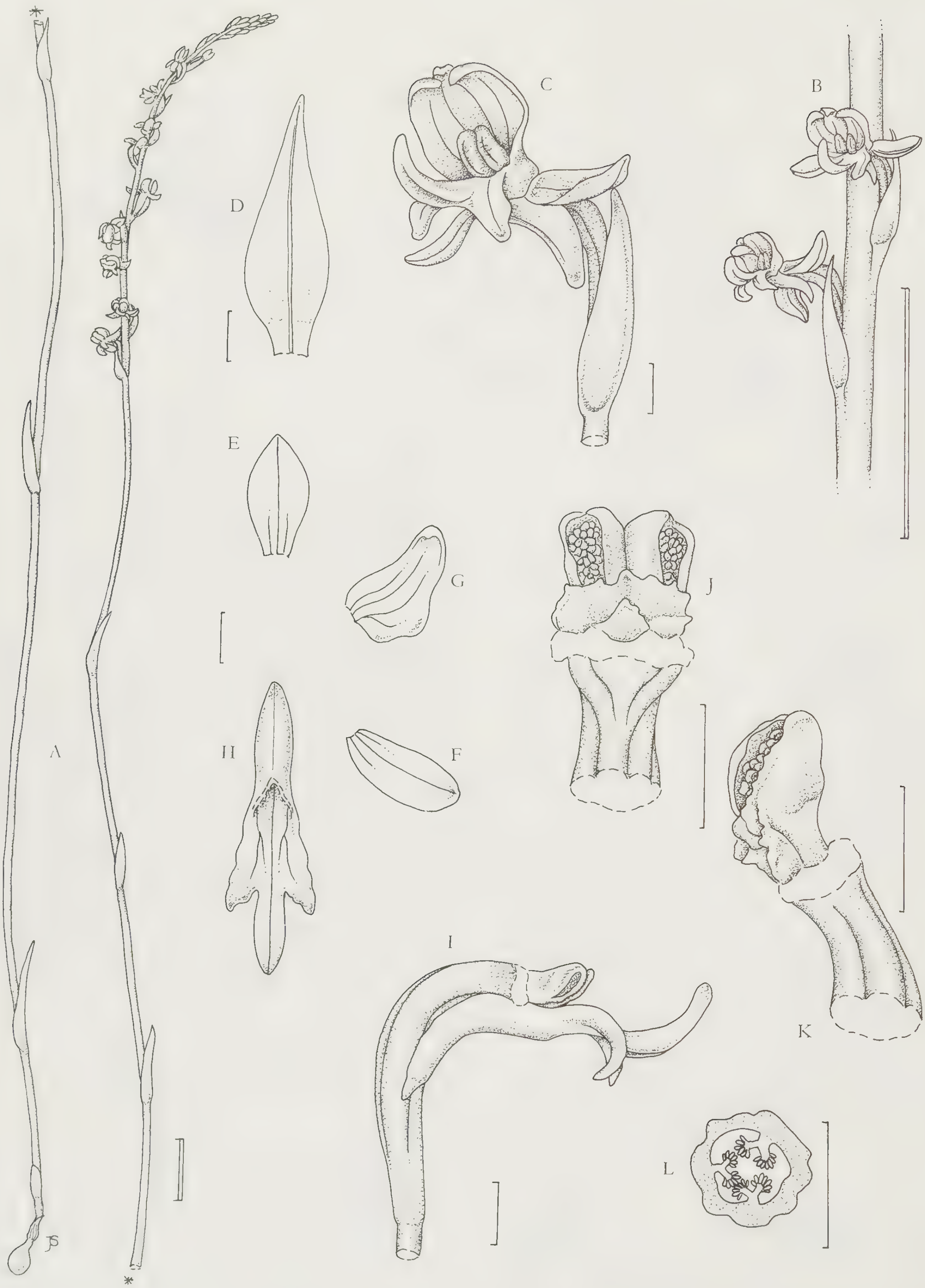

Fig. 63.1. *Benthamia praecox* Schltr. A. Habit; B. Inflorescence, portion; C. Flower; D. Bract; E. Dorsal sepal; F. Lateral sepal; G. Petal; H. Labellum; I. Labellum, column, and ovary, side view; J. Column, front view; K. Column, side view; L. Ovary, transection. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Nicoll s.n.* and Kew Spirit Collection no. 58663.

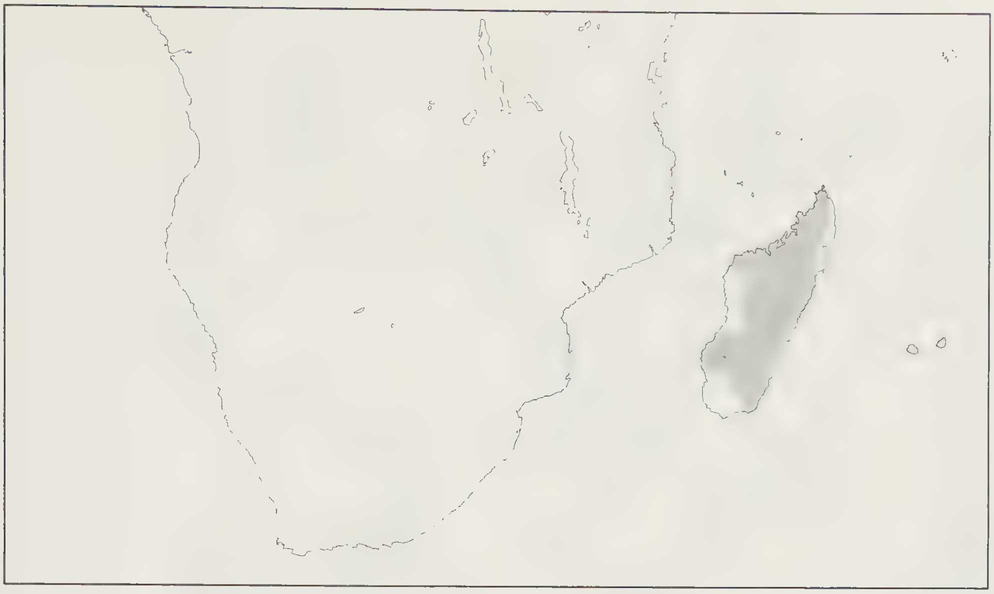

Fig. 63.2. Distribution map of *Benthamia.*

Cultivation

Compost C or E depending upon habitat. **(CB)**

Taxonomic notes

The most recent account of the genus is given by Perrier de la Bâthie (1939). An updated nomenclature is provided by Du Puy *et al.* (1999). **(PC)**

Taxonomic literature

Du Puy, D., Cribb, P. J., Bosser, J., Herman, J. and Herman, C. (1999). *Orchids of Madagascar.* Royal Botanic Gardens, Kew.

Perrier de la Bâthie, H. (1939). Orchidees. In *Flore de Madagascar* I. (ed. H. Humbert). Tananarive Imprimerie Officielle, Madagascar.

64. BONATEA

Bonatea Willd., *Sp. Pl.*, **4**, 43 (1805). Type species: *B. speciosa* (L.f.) Willd.

Habenaria sect. *Bonatea* (Willd.) Kränzl., *Orch. Gen. Sp.*, **1**, 178 (1901).

Derivation of name

Named in honour of M. Bonat, Professor of Botany at the University of Padua, Italy in the 19th century. **(PC)**

Description (Plate 84; Fig. 64.1)

Terrestrial *herbs* with elongated fleshy and tuberous roots. *Stem* unbranched, leafy. *Leaves* cauline, sometimes withered by flowering time, entire, green. *Inflorescence* terminal, one- to many-flowered. *Flowers* resupinate, green or yellow and white. *Dorsal sepal* free, usually forming hood with upper petal lobes. *Lateral sepals* united for some distance to base of lip, the lower petal lobes, and the stigmatic arms. *Petals* two-lobed, the upper lobe generally adnate to dorsal sepal, lower lobe adnate to stigmatic arms and lip. *Labellum* adnate to the column at the base, three-lobed above, usually with a tooth in the mouth of the spur; spur cylindrical, long or short. *Column* short; anther erect, loculi adjacent and parallel; canals usually±elongated, adnate to side lobes of rostellum; auricles entire, rugulose; pollinaria two, each with a sectile pollinium, a long slender caudicle and a small naked viscidium; stigmatic processes elongated, the lower part adnate to lip, free part club-shaped; rostellum standing out in front of anther, convex, three-lobed, with relatively short mid-lobe and often long, slender side lobes. **(PC)**

Distribution (Fig. 64.2)

A genus of about 20 species in mainland Africa, with one species in Yemen. **(PC)**

Ecology

Bonatea species grow in a range of dry habitats including dry grasslands, open deciduous woodland and scrub, hot, dry river valleys and coastal sand dunes (Schelpe 1966). *Bonatea antennifera*, for example, is often found in the drier areas of the Transvaal, such as around Johannesburg and Pretoria, and in the Waterberg district growing in the shade of thorn trees or bushes (Letty 1962). Members of the genus frequently occur at relatively high elevations of between 800 and 1500 m. In this respect, *B. pulchella* is unusual in that it grows at lower elevations of between 0 and 600 m. It grows in coarse, damp basic soil among rocks. Similarly, *B. cassidea* also occurs in shade among boulders (la Croix and Cribb 1995). *Bonatea speciosa* always grows in sandy soil and occurs on or near the beach in the eastern parts of South Africa (Pridgeon 1992).

Bonatea flowers in spring, summer, or early autumn at which time the leaves may have withered. The leafy aerial stem had previously developed from the tuber at the end of the dry season. Levels of fruit-set are not reported, but at least one flowering and fruiting specimen of *B. antennifera* was collected from near Kayne in Botswana in April 1978, where it grew at 1300 m with *Euclea undulata* Thunb. (Ebenaceae) (la Croix and Cribb 1995). **(RN)**

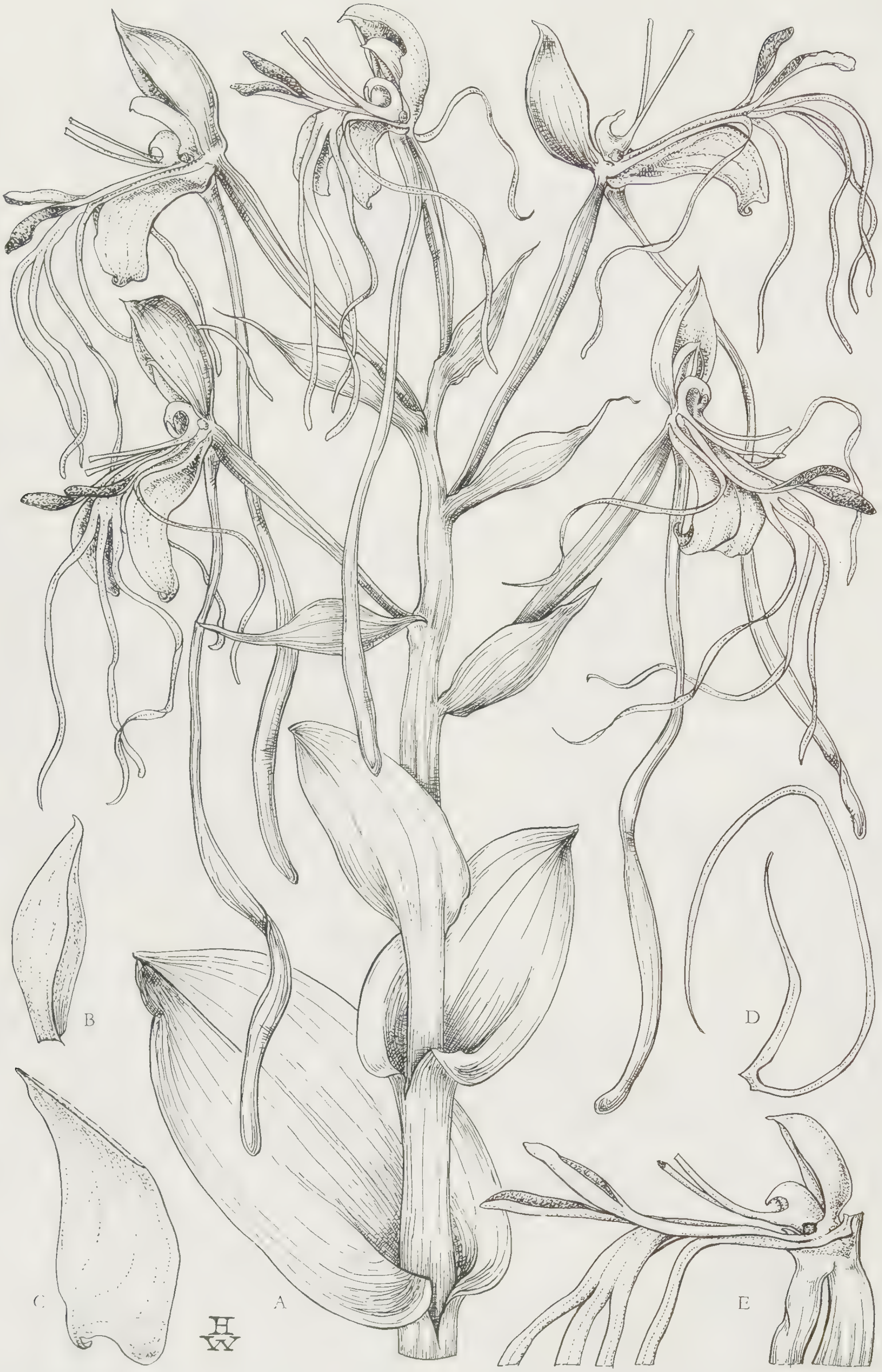

Fig. 64.1. *Bonatea steudneri* (Rchb.f.) T. Durand & Schinz. A. Inflorescence and upper part of stem, ×0.7; B. Dorsal sepal, ×1; C. Lateral sepal, ×1; D. Petal, ×1; E. Column, side view, sepals and petals removed, ×1. Drawn by Heather Wood from *Drummond & Hemsley 2523*.

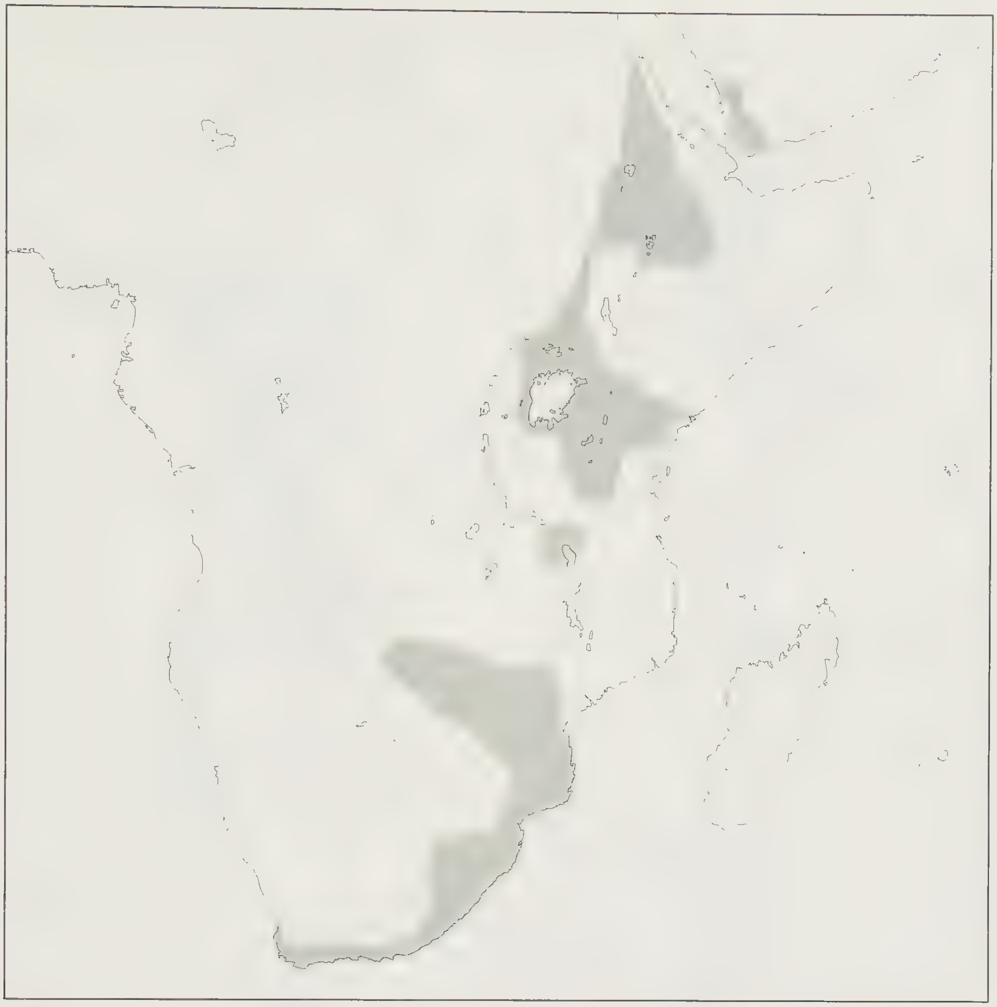

Fig. 64.2. Distribution map of *Bonatea.*

Uses

Bonatea are among the easiest African terrestrial orchids to grow. Several species are in cultivation, the most frequently seen being the South African *B. speciosa.*

Kokwaro (1976) listed the use of the crushed tubers of *Bonatea steudneri* Th. Dur. & Schinz (as *Habenaria steudneri* Rchb.f.) as a treatment for myiasis, stomach disorders, and influenza. Watt and Breyer-Brandwijk (1962) reported the use by Zulus in Natal of an infusion of the tubers of *B. foliosa* Lindl. (as *Habenaria foliosa* Rchb.f.) as an emetic. **(PC)**

Cultivation

Bonatea contains a number of showy tuberous terrestrials of easy cultivation. Compost B or C. **(CB)**

Taxonomic notes

Bonatea is closely allied to *Habenaria*, distinguished by its lateral sepals and the front lobe of the petals being joined to the lip and to the stigmatic arms in their lower parts and by the tooth in the mouth of the spur. Its relationship to *Habenaria* needs further investigation. **(PC)**

Taxonomic literature

Watt, J. M. and Breyer-Brandwijk, M. G. (1962). *Medicinal and poisonous plants of southern and eastern Africa* (2nd edn). Livingstone, Edinburgh and London.

65. BRACHYCORYTHIS

Brachycorythis Lindl., *Gen. Sp. Orch. Pl.*, 363 (1838). Type species: *B. ovata* Lindl.

Habenaria sect. *Phyllostachya* Benth. in Benth. & Hook.f., *Gen. Pl.*, **3**, 626 (1883). Type species not designated.

Platanthera sect. *Galeandriformes* Kränzl., *Orch. Gen. Sp.*, **1**, 610 (1898). Type species not designated.

Schwartzkopffia Kränzl., *Bot. Jahrb. Syst.*, **12**, 177 (1900). Type species: *S. buettneriana* Kränzl.

Phyllomphax Schltr., *Feddes Repert. Sp. Nov. Beih.*, **4**, 118 (1919). Type not designated.

Gyaladenia Schltr., *Beih. Bot. Centralbl.*, **38**, abt. 2, 124 (1921). Type species: *G. macowaniana* (Rchb.f.) Schltr.

Diplacorchis Schltr., *Beih. Bot. Centralbl.*, **38**, abt. 2, 127 (1921). Type species: *D. tenuior* (Rchb.f.) Schltr.

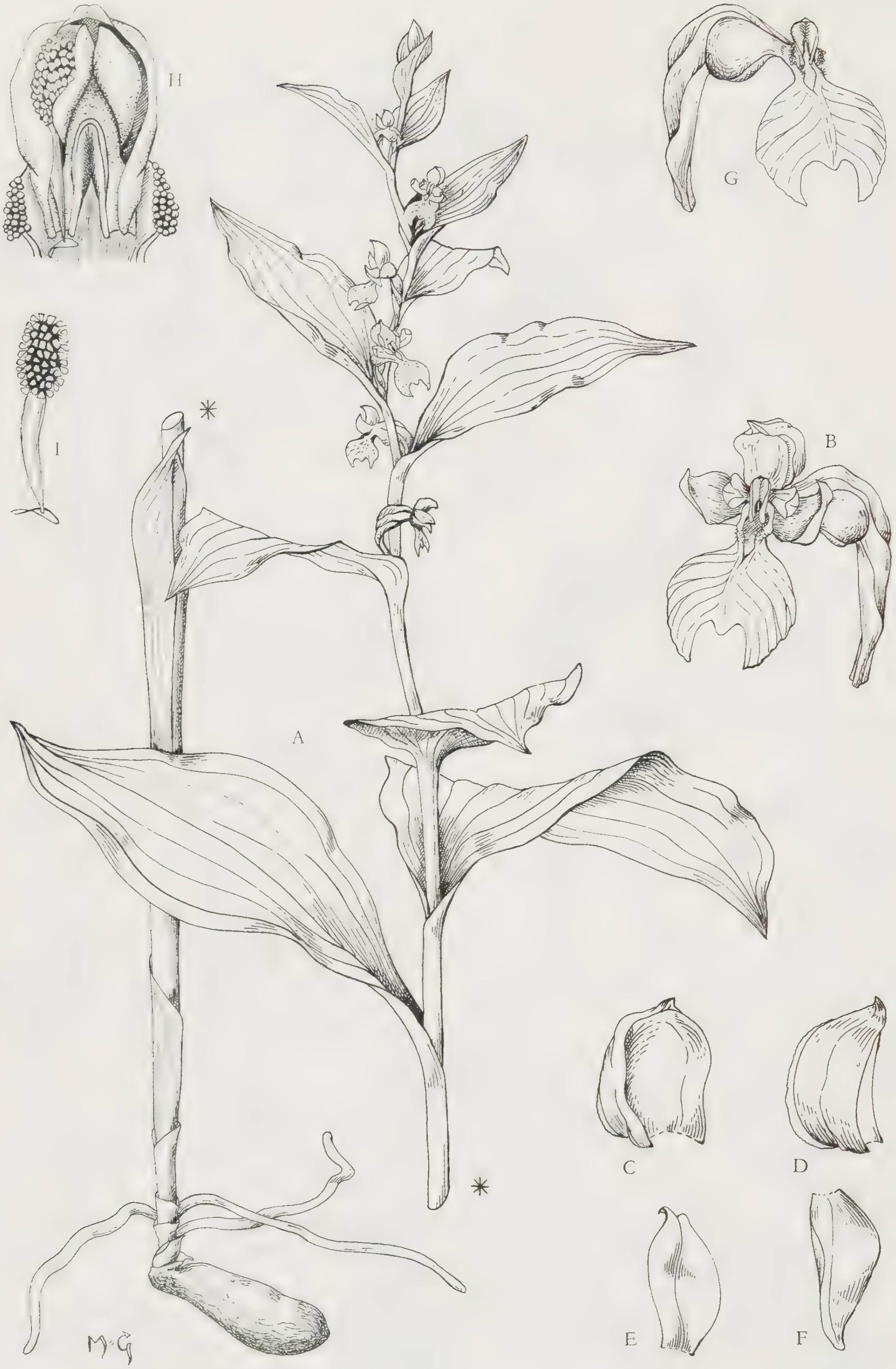

Fig. 65.1. *Brachycorythis tanganyikensis* Summerh. A. Habit, ×1; B. Flower, ×3; C. Dorsal sepal, front view, ×4; D. Dorsal sepal, side view, ×4; E. Lateral sepal, ×4; F. Petal, ×4; G. Labellum and column, front view, ×3; H. Column, front view, ×12; I. Pollinarium, ×12. Drawn by Mary Grierson from *Drummond & Hemsley 1871.*

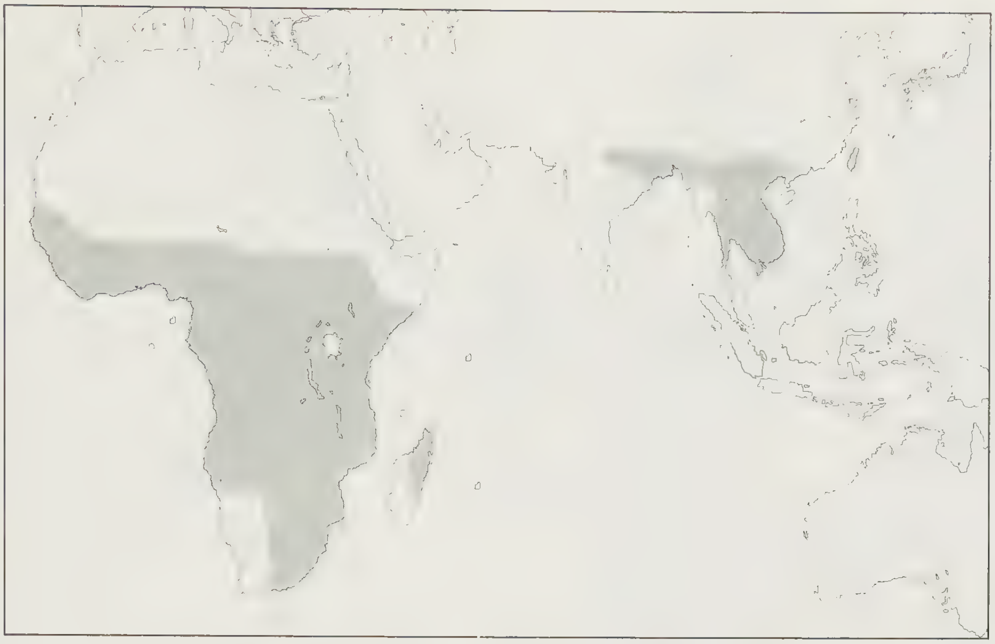

Fig. 65.2. Distribution map of *Brachycorythis*.

Derivation of name

From the Greek *brachys*, short, and *korys*, a helmet, in allusion to the helmet-shaped dorsal sepal and petals. **(PC)**

Description (Plate 85; Fig. 65.1)

Terrestrial, rarely epiphytic, *herbs* with fusiform or ellipsoid hairy tubers, rarely saprophytic terrestrial herbs. *Stems* leafy or rarely covered in scales. *Leaves* often numerous and overlapping, or rarely reduced to coloured scales. *Inflorescence* terminal, racemose, few- to many-flowered; bracts leaf-like and longer than the flowers at least at the base of the inflorescence. *Flowers* few to many in a terminal inflorescence, white, yellow, pink, mauve or purple often with darker spots. *Sepals* free, entire, the lateral sepals spreading and oblique. *Petals* usually adnate at the base to the side of the column, entire. *Labellum* bipartite; basal part (hypochile) spurred, saccate and boat-shaped; upper part (epichile) flattened, entire and 2–3 lobed, usually projecting forward; spur usually shorter than the labellum, sometimes saccate and obscure. *Column* erect, slender; anther loculi parallel, canals absent; pollinia two, granular; caudicles usually short; viscidia two, naked; stigma hollowed out; rostellum mid-lobe small, erect, folded; side lobes fleshy, short. **(PC)**

Distribution (Fig. 65.2)

A genus of 30–35 species, mainly occurring in tropical and South Africa, but with a few species from Madagascar and tropical and subtropical Asia across to Taiwan. **(PC)**

Cytogenetics

Brachycorythis helferi (Hook.f.) Summerh. and *B. obcordata* (Lindl.) Summerh. are based on x = 21 with $2n = 2x = 42$ chromosomes (Larsen 1966; Mehra & Kashyap 1978). **(SD)**

Ecology

Most *Brachycorythis* species are terrestrial herbs with tuberous roots, although a few species are epiphytic, e.g. *B. kalbreyeri*. They grow in a variety of habitats that are usually quite wet including marshy/ boggy grassland, grassy swamps, damp pastures, marshes in forests, seepage areas among rocks, riverine forest and rainforest, wet (or dry) dambo, and scrubby, deciduous and *Brachystegia* (Fabaceae) woodland. In some cases the habitats are permanently wet, as in central Africa (*B. angolensis*), but other times they are seasonally wet, as in upland grassland in Zambia and Angola (*B. mixta*) according to Summerhayes (1968) and la Croix and Cribb (1995). *Brachycorythis* species also grow in the moist grasslands in the summer rainfall area of South Africa (Schelpe 1966). Typical substrates in which the terrestrial species grow include clay or sandy soil and on granite outcrops (Summerhayes 1968; la Croix and Cribb 1995), and they occur at elevations ranging from 500 to 2200 m, sometimes in montane habitats such as upland grassland. *Brachycorythis* is sporadic in the South African part of its range, and usually only one or two plants occur at a site (Schelpe 1966). Flowering of *Brachycorythis* takes place in the summer between October and February. An indication that some fruit-set occurs is the existence of a fruiting herbarium specimen of *B. rhodostachys* collected from Zambia in November 1962 (la Croix and Cribb 1995). **(RN)**

Uses

Brachycorythis ovata Lindl. has been used as a charm in southern Africa (Rayner 1977). **(PC)**

Cultivation

Compost C is recommended. **(CB)**

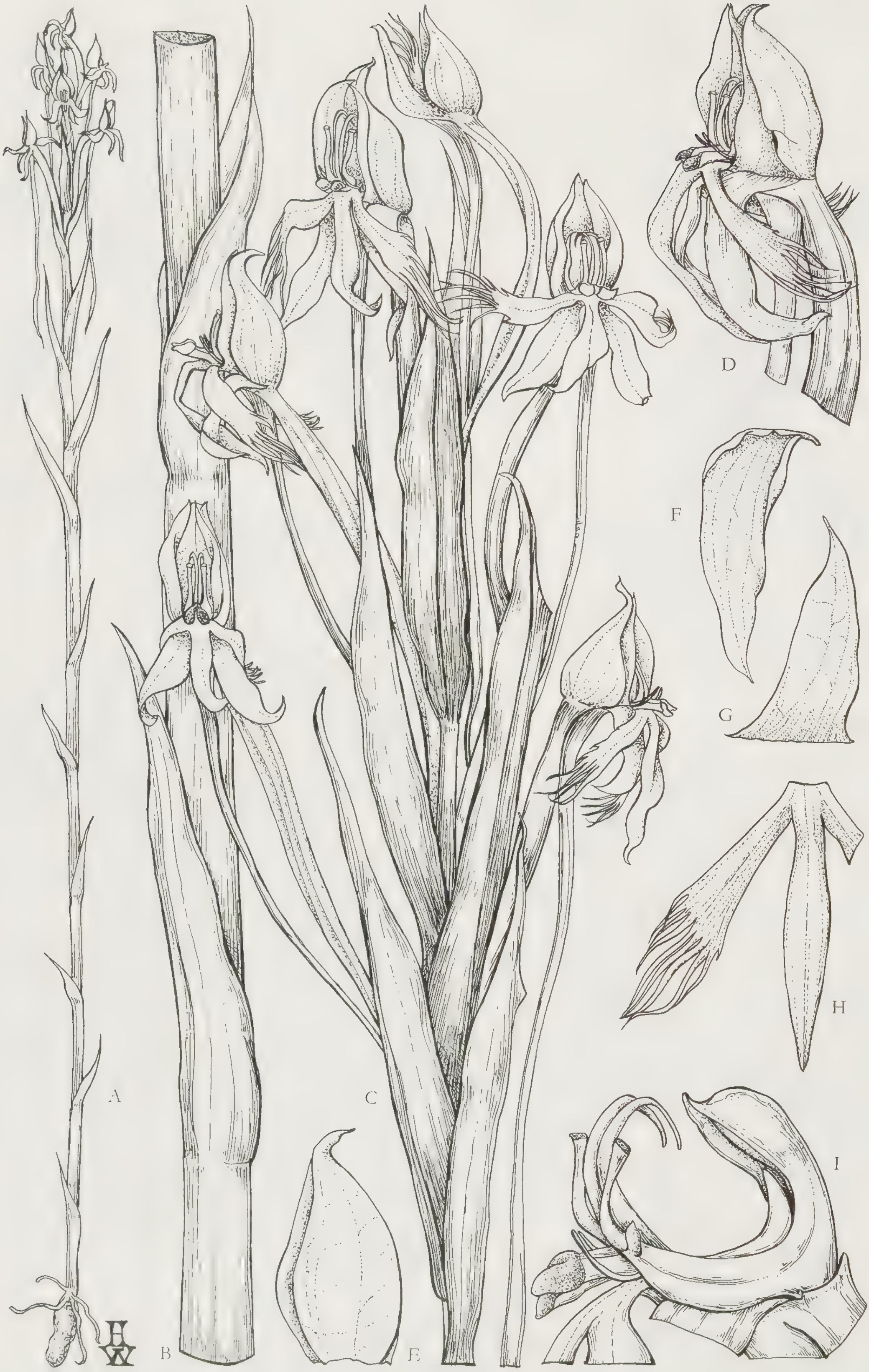

Fig. 66.1. *Centrostigma occultans* Schltr. A. Habit, ×0.25; B. Stem, portion, ×1; C. Inflorescence, ×1; D. Flower, ×1.5; E. Dorsal sepal, ×2; F. Lateral sepal, ×2; G. Petal, ×2; H. Labellum (one lobe removed), ×2; I. Column, side view, sepals and petals removed., ×3. Drawn by Heather Wood from *Holmes 95*.

Taxonomic notes

Summerhayes (1955) revised *Brachycorythis*, listing 33 species. He synonymized related genera proposed by Kränzlin and Schlechter and did not recognize any infrageneric groupings. He did, however, retain the concept of *Schwartzkopffia* on the basis that its species are leafless saprophytes with only brownish cataphylls, despite the fact that its labellum has a hollowed-out hypochile and epichile like that of *B. ovata*. Until more material of of *Brachycorythis* is available for molecular studies, we are synonymizing *Schwartzkopffia* under it on the basis of this distinctive labellum. **(PC)**

Taxonomic literature

Rayner, E. (1977). Orchids and medicine. *South African Orchid Journal*, **8**, 120.

Summerhayes, V. S. (1955). A revision of the genus *Brachycorythis*. *Kew Bulletin*, **10**, 221–64.

66. CENTROSTIGMA

Centrostigma Schltr., *Bot. Jahrb. Syst.*, **53**, 522 (1915). Type species: *C. occultans* (Rchb.f.) Schltr. Lectotype selected by Summerhayes, *Kew Bull.*, **11**, 219 (1951).

Derivation of name

From the Greek *centrum*, centre, and *stigma*, a stigma, in reference to the central position of the stigma in the flower. **(PC)**

Description (Plate 86; Fig. 66.1)

Terrestrial *herbs* with tuberous roots. *Stems* unbranched, leafy. *Leaves* cauline, entire, green. *Inflorescence* terminal, laxly to subdensely few- to many-flowered. *Flowers* resupinate, white, yellowish, or green. *Sepals* and *petals* free, entire. *Labellum* joined to column at the base, three-lobed; side lobes entire or with pectinate teeth; spur cylindrical. *Column* erect, anther loculi adjacent, parallel, canals slender and upcurved; auricles small, entire; pollinaria two, each with a sectile pollinium, caudicle, and small naked viscidium; stigmatic processes two-lobed above the base, the lower lobe receptive, porrect, clavate or capitate; upper lobe sterile, projecting upward in front of the anther, often slender and horn-like; rostellum three-lobed, the midlobe narrowly triangular, erect between the anther loculi but shorter than the anther, the side lobes porrect or upcurved. **(PC)**

Distribution (Fig. 66.2)

A genus of three species in tropical Africa. **(PC)**

Ecology

Members of the tropical African genus *Centrostigma* are all terrestrial herbs with tubers and are either tall robust plants (e.g. *C. clavatum*) or shorter, slender ones (*C. papillosum*). They inhabit dambo and swampy/marshy grasslands and grow at relatively high elevations of 1200–1700 m. Flowering of *Centrostigma* takes place between November and January (la Croix and Cribb 1995). **(RN)**

Uses

None recorded. **(PC)**

Cultivation

Compost C or D. **(CB)**

Taxonomic notes

Centrostigma is closely related to *Habenaria*, differing in the stigmas that are differentiated into two elongated arms, the lower clavate and fertile, the upper sterile and horn-like. All three species occur in the *Flora Zambesiaca* region (la Croix and Cribb 1995). **(PC)**

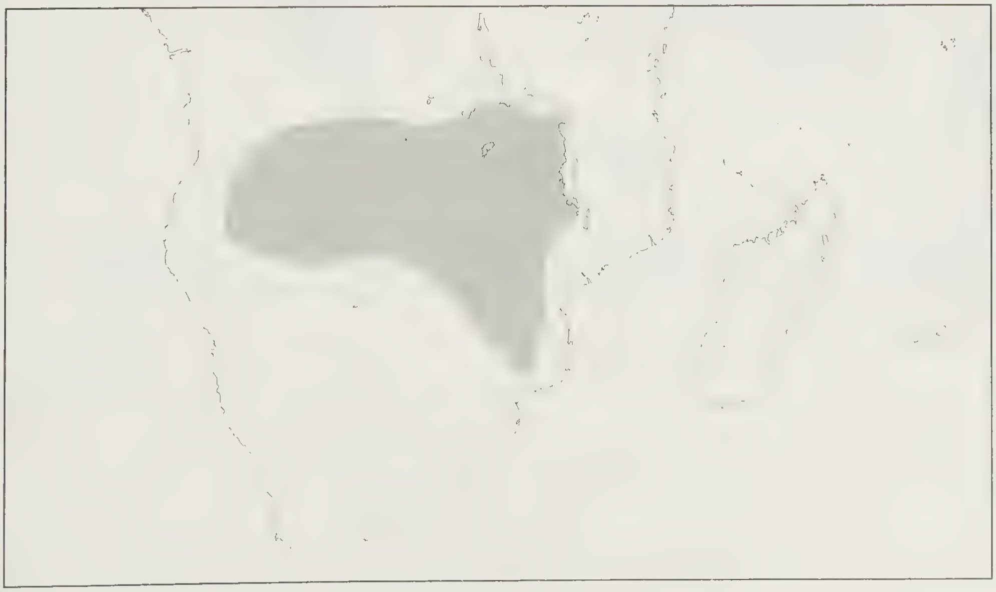

Fig. 66.2. Distribution map of *Centrostigma*.

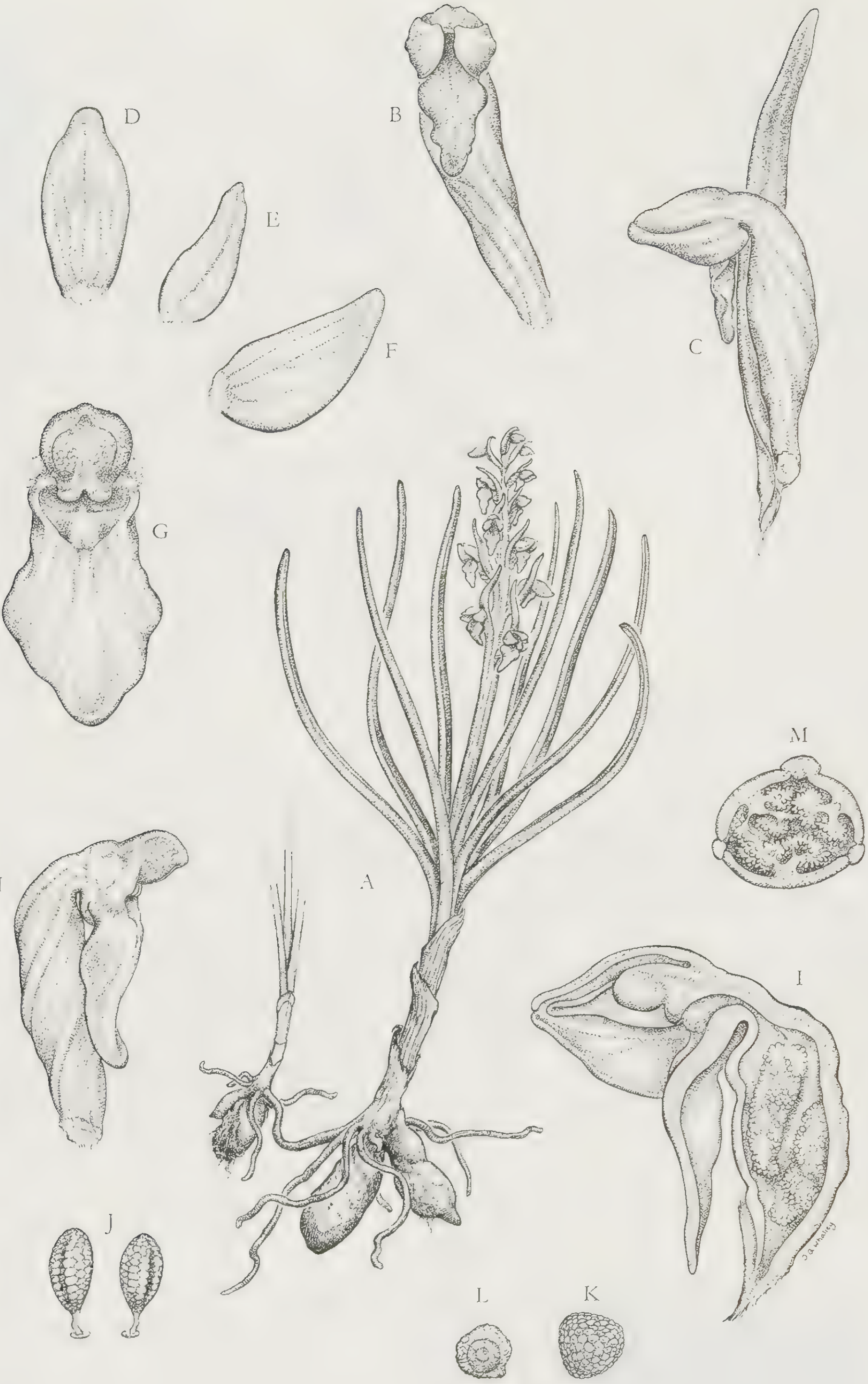

Fig. 67.1. *Chamorchis alpina* (L.) Rich. A. Habit, ×1; B. Flower from front, ×6; C. Flower and bract from side, ×6; D. Dorsal sepal, ×9; E. Petal, ×9; F. Lateral sepal, ×9; G. Labellum and column, ×15; H. Flower from side, perianth removed, ×12; I. Flower with ovary, longitudinal section; J. Pollinaria, ×15; K. Pollinaria, ×70; L. Pollen grain, ×360; M. Ovary, transverse section, ×9. Drawn by Oliver Q. Whalley from Kew Spirit Collection nos. 40942, 22532, 41240, and 22533.

Taxonomic literature

la Croix, I. and Cribb, P. J. (1995). *Centrostigma* Schltr. In *Flora Zambesiaca* (ed. G. V. Pope), **11** (1), 48–50.

67. CHAMORCHIS

Chamorchis Rich., *Mém. Mus. Paris*, **4**, 49 (1818), as *Chamaeorchis*. Type species: *Chamorchis alpina* (L.) Rich.

Chamaerepes Spreng., *Syst. Veget.*, **3**, 702 (1826). Type species: *Chamorchis alpina* (L.) Spreng. (= *Chamorchis alpina* (L.) Rich.)

Derivation of name

From the Greek *chamai*, dwarf, and *orchis*, orchid, with reference to the diminutive size of the plant. **(JW)**

Description (Plate 87; Fig. 67.1)

Dwarf *herb. Rootstock* tuberous, tubers two, oblong or ellipsoid, subsessile or shortly stipitate. *Stem* erect, lacking scale leaves. *Leaves* all basal, 6–10, linear, terete, unspotted. *Inflorescence* short, lax to somewhat densely 6–14 flowered; floral bracts herbaceous. *Flowers* small, resupinate, yellowish green. *Sepals* and *petals* connivent, forming a hood, petals slightly shorter. *Labellum* slightly longer than sepals and petals, ovate to oblong-ovate, shallowly three lobed or entire, with two basal swellings forming a nectariferous recess, spur absent. *Column* minute; rostellum minute, triangular, margin slightly incurved; pollinia two; viscidia large. *Ovary* sessile, twisted, glabrous. **(JW)**

Distribution (Fig. 67.2)

A monospecific genus distributed in northern and alpine Europe, north to Russia, east to the Carpathians. **(JW)**

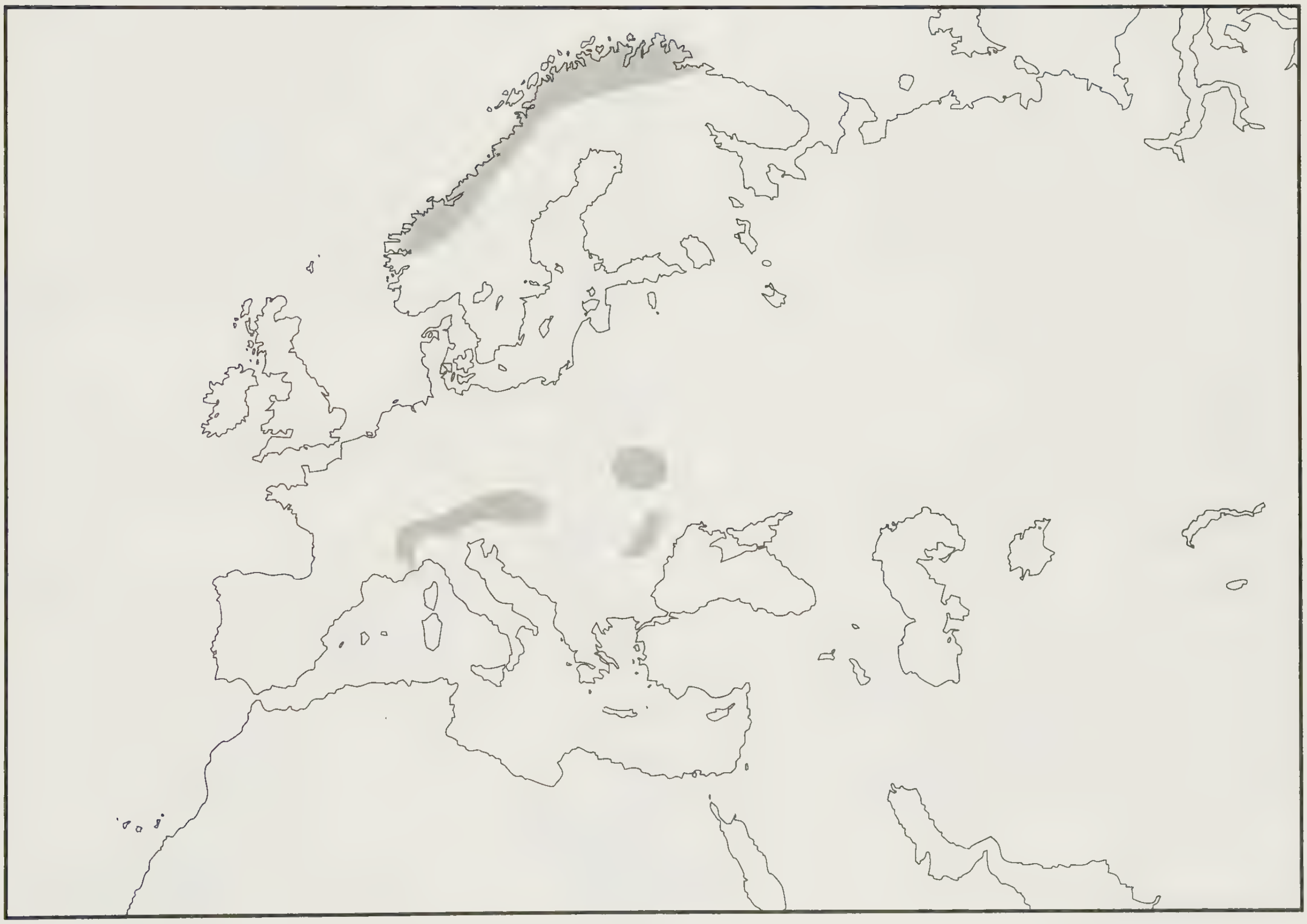

Fig. 67.2. Distribution map of *Chamorchis*.

Palynology

Pollen morphology of *C. alpina* is reticulate with fragmented muri (Schill and Pfeiffer 1977). **(AP)**

Cytogenetics

In *Chamorchis* the basic number is x = 21. *Chamorchis alpina* has a diploid number of $2n = 42$ with a moderately asymmetric karyotype (D'Emerico *et al.*, unpublished). **(SD)**

Phytochemistry

Infection of the tubers of *C. alpina* with a strain of *Rhizoctonia repens* from *Orchis militaris* results in the synthesis of the phytoalexin orchinol (2,4-dimethoxy-7-hydroxy-9,10-dihydrophenanthrene) and *p*-hydroxybenzylalcohol. This observation was made as part of a survey of orchinol and *p*-hydroxybenzylalcohol production in a number of species representing genera in subtribe Orchidinae (Nüesch 1963; Gaumann *et al.* 1960). **(NV, RG)**

Ecology

Chamorchis alpina grows in mountain pastures and meadows in dry or damp calcareous soils and in full sunlight. In the Alps it occurs at (1500–) 2000–2700 m but is found at much lower elevations in Scandinavia, e.g. in Lapland where it grows in exposed heathland (Davies *et al.* 1988). *Chamorchis* flowers from July to August in alpine meadows, where it often grows with edelweiss (*Leontopodium alpinum* Cass.; Asteraceae) and mountain avens (*Dryas octopetala* L.; Rosaceae). It can be very difficult to see because of its green flower colour, grass-like basal leaves, and small stature, which may have contributed to its reputation as a rare orchid (Davies *et al.* 1988). At the local level, it can sometimes be very abundant and grow in large populations of several hundred plants, most probably due to active vegetative propagation of the tubers. **(RN)**

Pollination

The minute flowers of *C. alpina* provide nectar in a ridge on the labellum. A spur is absent. Flower visitors presumably are small insects, but detailed observations have not been reported. High seed set, however, indicates that flowers are either pollinated efficiently by insects or self-pollination, the latter possibility suggested by Reinhard *et al.* (1991). **(AW, SC, AD)**

Uses

None recorded. **(JW)**

Cultivation

Throughout its range *Chamorchis* grows primarily in damp pastures over limestone. It should be grown in containers of compost C. **(CB)**

68. CHONDRADENIA

Chondradenia Maxim. ex F. Maek., *Wild Orch. Japan in Colour*, 456 (1971). Type species: *Chondradenia fauriei* (Finet) T. Sawada.

Derivation of name

From the Greek *chondros*, cartilage, and *aden*, a gland, in reference to the elongated viscidium. **(JW)**

Description (Fig. 68.1)

Perennial sympodial *herbs*. *Rootstock* fibrous, fleshy, pilose. *Tubers* absent. *Stem* short, with two cataphylls. *Leaves* basal, one or two, ovate, attenuate at base, obtuse or mucronate-apiculate, unspotted. *Inflorescence* densely (2) 3–6-flowered, erect or nodding, terminal; peduncle naked; rachis short; floral bracts leafy, lowermost often longer than flowers. *Flowers* resupinate, white with a basal yellow area on labellum, or pink. *Sepals* and *petals* free. *Sepals* ovate-truncate, oblong, elliptic, or obliquely lingulate, acute or obtuse, sometimes apically serrulate. *Petals* cuneate or narrowly triangular-ovate, acute or obtuse. *Labellum* spurred, ovate-lanceolate, cuneate at base, emarginate with a small central tooth, or subobtuse, deflexed or spreading, spur ovoid to globose, much shorter than ovary. *Column* short; stigma linear, transverse, lobes separate; rostellum three-lobed, plicate, side lobes triangular, acute, porrect, mid-lobe deflexed; anther elliptic, loculi parallel; pollinia two, attached to a solitary naked, elongate viscidium; bursicle absent. *Ovary* shortly pedicellate (in *C. fauriei*; ? *C. doyonensis*). *Capsule* obovate, slightly incurved at apex. **(JW)**

Distribution (Fig. 68.2)

Two species distributed in Japan (Honshu) and on the border between Myanmar and south-west China (Yunnan). **(JW)**

Ecology

Chondradenia is a terrestrial herb that grows on mica-schist in montane grassland at 3500–4200 m, as in Honshu, Japan, where it is a rare species (Ohwi 1965). **(JW, RN)**

Uses

None recorded. **(JW)**

Cultivation

Unknown in cultivation, but compost D in containers may be tried. **(CB)**

Taxonomic literature

Brieger, F. G., Maatsch, R., and Senghas, K. (1973). 42. *Chondradenia*. In *Rudolf Schlechter: Die Orchideen 3. Völlig neubearbeitete auflage* (ed. F. G. Brieger, R. Maatsch, K. Senghas), **4**, 239.

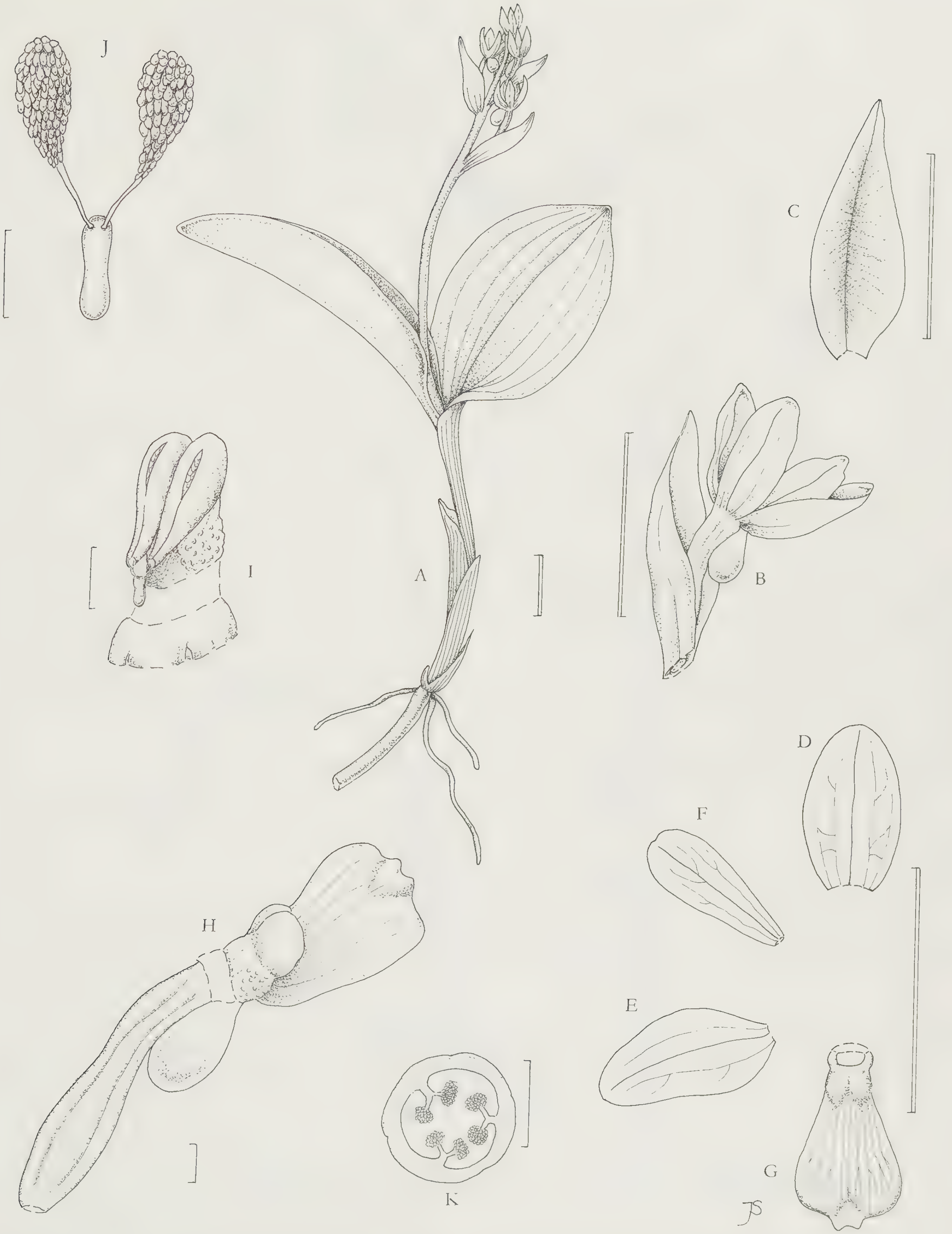

Fig. 68.1. *Chondradenia fauriei* (Finet) T. Sawada ex F. Maek. A. Habit; B. Flower; C. Bract; D. Dorsal sepal; E. Lateral sepal; F. Petal; G. Labellum; H. Labellum and column, side view; I. Column, oblique view; J. Pollinarium. K. Ovary, transection. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Faurie 13432*.

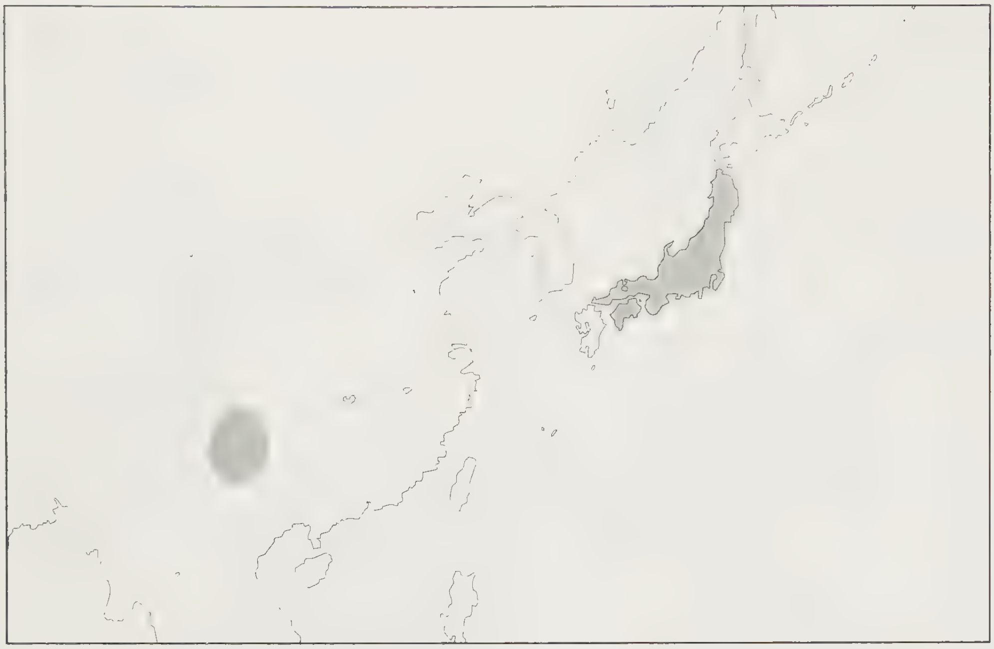

Fig. 68.2. Distribution map of *Chondradenia.*

Finet, A. (1898). Orchidées nouvelles ou peu connues. *Journal de Botanique*, **12**, 340–1, plate V, A-K.

Handel-Mazzetti, H. (1936). *Symbolae Sinicae*; botanische ergebnisse der expedition der akademie der wissenschaften in Wien nach südwest-China 1914/1918. **7.** *Anthophyta*, 1324.

Makino, T. (1902). Observations on the flora of Japan. *The Botanical Magazine, Tokyo*, **16**, 89.

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69. COMPERIA

Comperia C. Koch, *Linnaea*, 22, 287 (1849); Taubenheim, *Orchidee*, **31**, 5–10 (1908). Type species: *Comperia comperiana* (Steven) Asch. & Graebn.

Orchis sect. *Comperia* (C. Koch) Kränzl., *Orch. Gen. Sp.*, **1**, 115 (1901).

Derivation of name

Named after D. Compère, a Crimean landowner who collected the type material. **(JW)**

Description (Plate 88; Fig. 69.1)

Rather robust *herb. Rootstock* tuberous, tubers entire, ovate-oblong or ellipsoid, sessile. *Stem* erect, leafy below, glabrous. *Leaves* unspotted. *Inflorescence* few- to many-flowered, lax to somewhat dense; floral bracts membranous. *Flowers* large and showy, greenish, suffused brownish purple or rose, erect to spreading. *Sepals* and *petals* connivent to form a hood, free at apex. Petals linear, with 1 or 2 marginal teeth. *Labellum* expanded from a broadly triangular-cuneate, incurved base into four long filiform segments, total length 4–10 cm, spur cylindrical, slightly shorter than ovary, decurved. *Column* short; rostellum three-lobed, median lobe short, lamelliform; pollinia two, caudicles attached to separate viscidia, both enclosed in a single bursicle. *Ovary* cylindrical to fusiform, subsessile, slightly twisted, glabrous. **(JW)**

Distribution (Fig. 69.2)

A monospecific genus distributed in the eastern Aegean Isles, Crimea, Syria, Lebanon, Turkey, Caucasus, and western Iran. **(JW)**

Ecology

Comperia comperiana grows on dry calcareous soils in mountainous areas from 400 m–2000 m. The most typical habitats for *Comperia* are open pinewoods where it grows in semi-shade, although it also occurs in deciduous woods and rarely in grassland (Davies *et al.* 1988; Delforge 1995). On Lesbos, for example, one of its few known sites on the island is on the edge of pinewoods on the slopes of Mt Olympus at 950 m (Raine 1990). The flowering period of *Comperia* is between April and July or August and is influenced by the elevation at which it grows. For example, although in Rhodes, Lesbos, and western Turkey flowering normally commences in mid- to late April, in the mountains of Lebanon peak flowering is in late May (Davies *et al.* 1988). *Comperia* is regarded as being a local and rare orchid within its range and, although some large colonies have been found, most populations are small and widely dispersed. It is known to have grown at particular localities for a long time; on Lesbos it has been recorded growing since the 19th century (Davies *et al.* 1988). **(RN)**

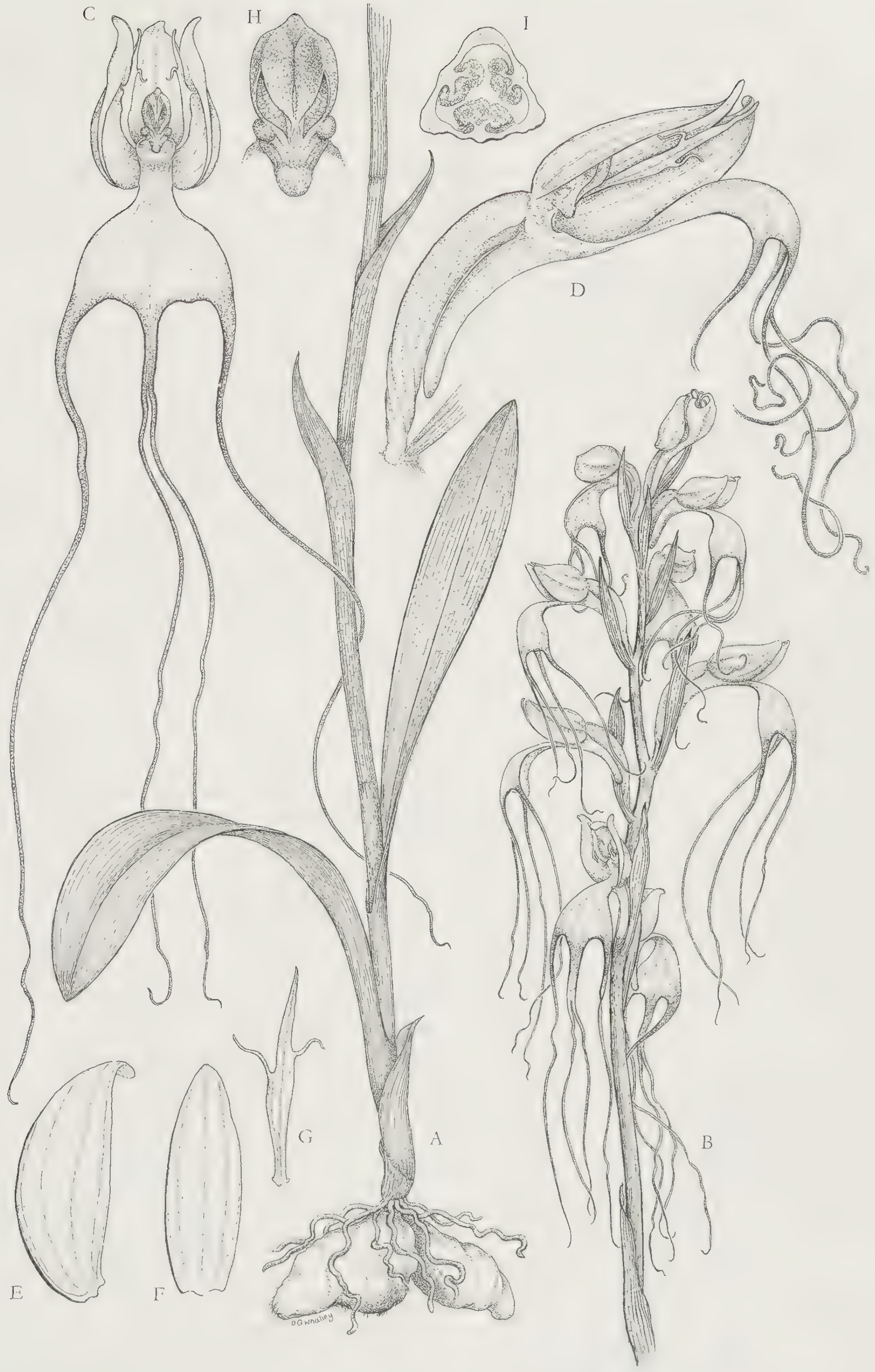

Fig. 69.1. *Comperia comperiana* (Steven) Asch. & Graebn. A. Habit, ×1; B. Inflorescence, ×1; C. Flower from front, ×3; D. Flower from side (one lateral sepal removed), ×3; E. Lateral sepal, ×3; F. Dorsal sepal, ×3; G. Petal, ×3; H. Anther, ×6; I. Ovary, transverse section, ×6. Drawn by Oliver Q. Whalley from Kew Spirit Collection no. 39448.

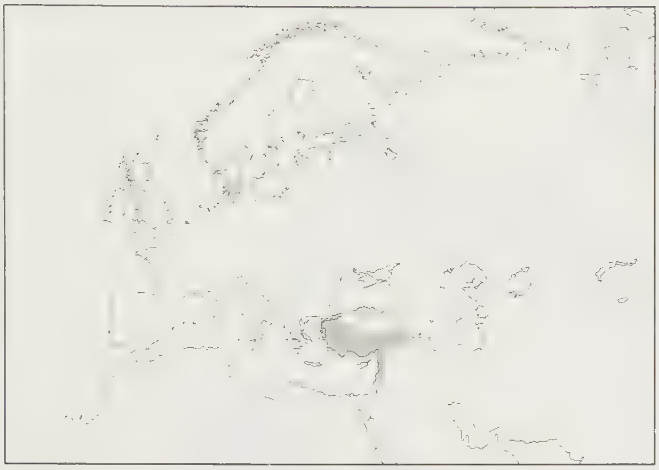

Fig. 69.2. Distribution map of *Comperia.*

Uses

Comperia is under threat from collectors as in Turkey, where it has been traditionally used in the production of salep ice cream (Delforge 1995). **(RN)**

Cultivation

Comperia comperiana occurs in woodland over limestone. It should be grown in containers of compost C with added lime. **(CB)**

70. CYNORKIS

Cynorkis Thouars, *Nouv. Bull. Sci. Soc. Philom. Paris*, **1**, 317 (1809). Type species: *C. fastigiata* Thouars. Lectotype selected by Cribb in Bechtel *et al.*, *Man Cult. Orch. Sp.*, 108 (1981).

Cynosorchis Thouars, *Orch. Iles Afr.*, tt. 13–15 (1822), *sphalm. pro Cynorkis.*

Amphorkis Thouars, *Nouv. Bull. Sci. Soc. Philom. Paris*, **1**, 316 (1809), *nom. superfl.*

Amphorchis Thouars, *Orch. Iles Afr.*, tt. 13–15 (1822), *sphalm. pro Amphorkis.*

Arnottia A. Rich., *Mem. Soc. Hist. Nat. Paris*, **4**, 29 (1828) & *Orch. Iles Fr. Bourb.*, 33, t. 7 (18); Benth. & Hook.f., *Gen. Pl.*, **3**, 622 (1883). Type species: *A. mauritiana* A. Rich.

Bicornella Lindl., *Gen. Spec. Orch. Pl.*, 334 (1835). Type species not designated

Hemiperis Frappier in Cordemoy, *Fl. Reunion*, 235 (1895). Type species not designated.

Camilleugenia Frappier in Cordemoy, *Fl. Reunion*, 234 (1895). Type species: *C. coccinelloides* Frappier ex Cordem.

Helorchis Schltr., *Feddes Repert. Sp. Nov.*, **33**, 35 (1925). Type species: *Helorchis filiformis* (Kränzl.) Schltr. [*Peristylus filiformis* Kränzl.].

Microtheca Schltr., *Feddes Repert. Sp. Nov.*, **33**, 76. (1925). Type species: *M. madagascarica* Schltr.

Lemuranthe Schltr., *Feddes Repert. Sp. Nov.*, **33**, 84. (1925). Type species: *L. gymnochiloides* (Schltr.) H. Perrier [*Habenaria gymnochiloides* Schltr.].

Derivation of name

From the Greek *kynos*, a dog, and *orchis*, an testicle, referring to the tubers, which resemble the testicles of a dog. **(PC)**

Description (Plate 89; Fig. 70.1)

Terrestrial, or occasionally epiphytic, *herbs* with fleshy or tuberous roots. *Stem*, ovary and calyx often with glandular hairs. *Leaves* one to several, radical, with a few sheath-like and cauline, sometimes with distinctively coloured veins. *Inflorescence* terminal, one- to many-flowered, racemose. *Flowers* usually resupinate, pink, mauve, or purple, occasionally white or yellow. *Sepals* free or slightly adnate to the labellum, the dorsal often forming a hood with the *petals*, the lateral sepals spreading. *Labellum* entire or 3–5 lobed, spurred at the base. *Column* short and broad; androclinium erect or sloping; anther loculi parallel, the canals short or long and slender; viscidia two, rarely one, lateral appendages distinct; stigmatic processes oblong, papillose, usually joined to the lobes of the rostellum; side lobes of rostellum usually elongated; mid-lobe often large, projecting forward. *Capsules* oblong or fusiform, often ripe at the base of an inflorescence that is still flowering at the apex. **(PC)**

Distribution (Fig. 70.2)

A genus of about 125 species, mostly native to Madagascar and the Mascarene Islands, with up to 20 species on mainland Africa. **(PC)**

Infrageneric treatment (PC)

Six sections were recognized by Perrier de la Bâthie (1931), but this publication, cited by Perrier (1939), was never published:

Cynorkis section **Hemiperis (**Frappier) H. Perrier, *Arch. Bot. Caen* 5, *Bull. Mens.*, 36 (1931 but unpubl.) and *Fl. Madagascar* 49. *Orch.*, **1**, 74 (1939) (as *Cynosorchis*);

Cynorkis section **Lowiorchis** H. Perrier, *Arch. Bot. Caen* 5, *Bull. Mens.*, 53 (1931 but unpubl.) and *Fl. Madagascar* 49. *Orch.*, **1**, 74 (1939) (as *Cynosorchis*);

Cynorkis section **Gibbosorchis** H. Perrier, *Arch. Bot. Caen* 5, *Bull. Mens.*, 56 (1931 but unpubl.) and *Fl. Madagascar* 49. *Orch.*, **1**, 74 (1939) (as *Cynosorchis*);

Cynorkis section **Imerinorchis** H. Perrier, *Arch. Bot. Caen* 5, *Bull. Mens.*, 66 (1931 but unpubl.) and *Fl. Madagascar* 49. *Orch.*, **1**, 74 (1939) (as *Cynosorchis*);

Cynorkis section **Lemuranthe** H. Perrier, *Arch. Bot. Caen* 5, *Bull. Mens.*, 65 (1931 but unpubl.) and *Fl. Madagascar* 49. *Orch.*, **1**, 74 (1939). Type species: *C. gymnochiloides* (Schltr.) H. Perrier (as *Cynosorchis*);

Cynorkis section **Monadeniorchis** H. Perrier, *Arch. Bot. Caen* 5, *Bull. Mens.*, 36 (1931 but unpubl.) and *Fl. Madagascar* 49. *Orch.*, **1**, 74 (1939). Type species: *C. monadenia* H. Perrier (as *Cynosorchis*).

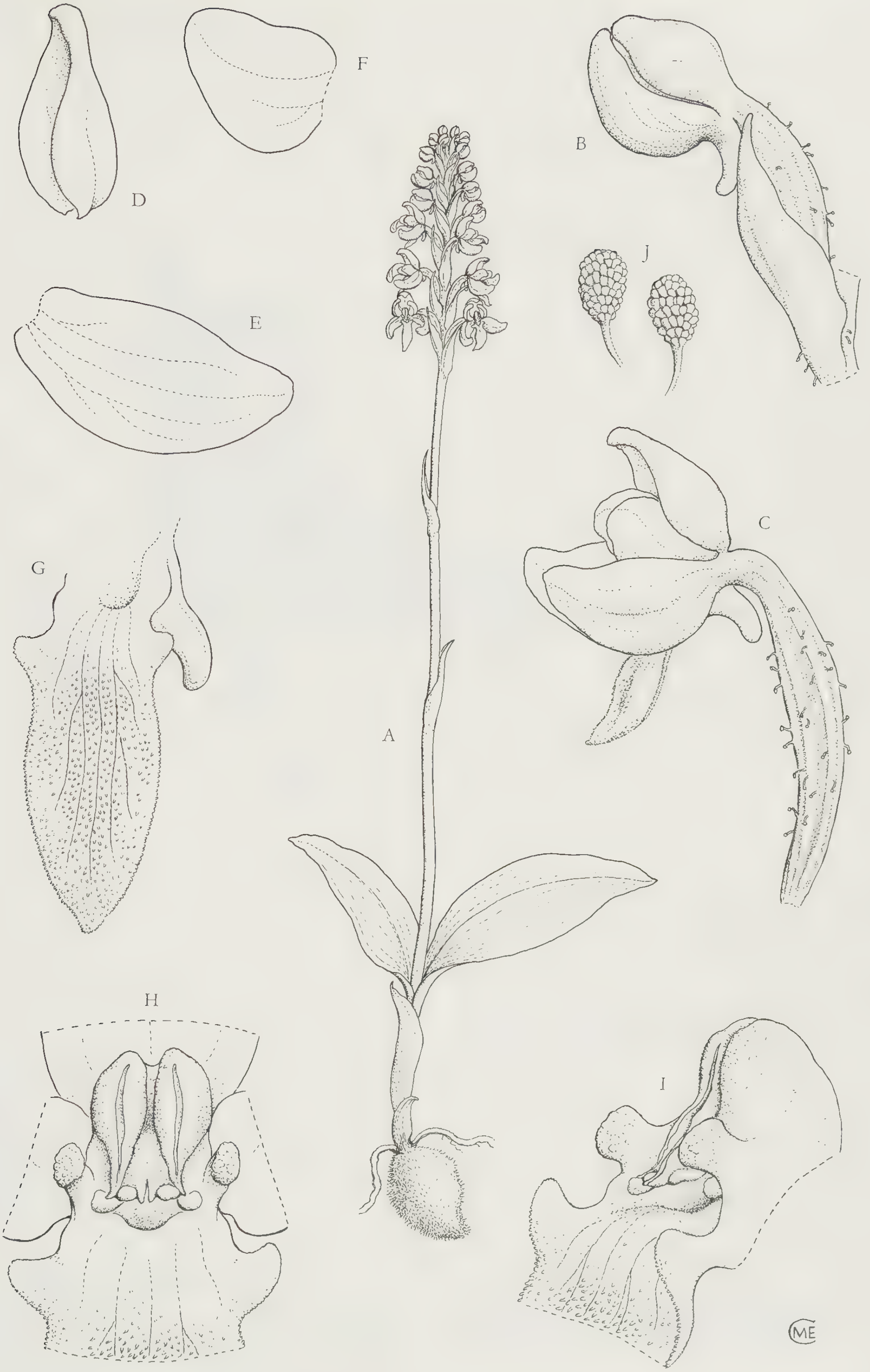

Fig. 70.1. *Cynorkis brevicalcar* P. J. Cribb. A. Habit, ×1; B. Flower bud, ×8; C. Flower, ×8; D. Dorsal sepal, ×10; E. Lateral sepal, ×10; F. Petal, ×10; G. Labellum, front view, ×12; H. Column, front view, ×24; I. Column, side view, ×30. J. Pollinia, ×36. Drawn by M. Church from *Blackmore et al. 374* and *Brummitt 9652*.

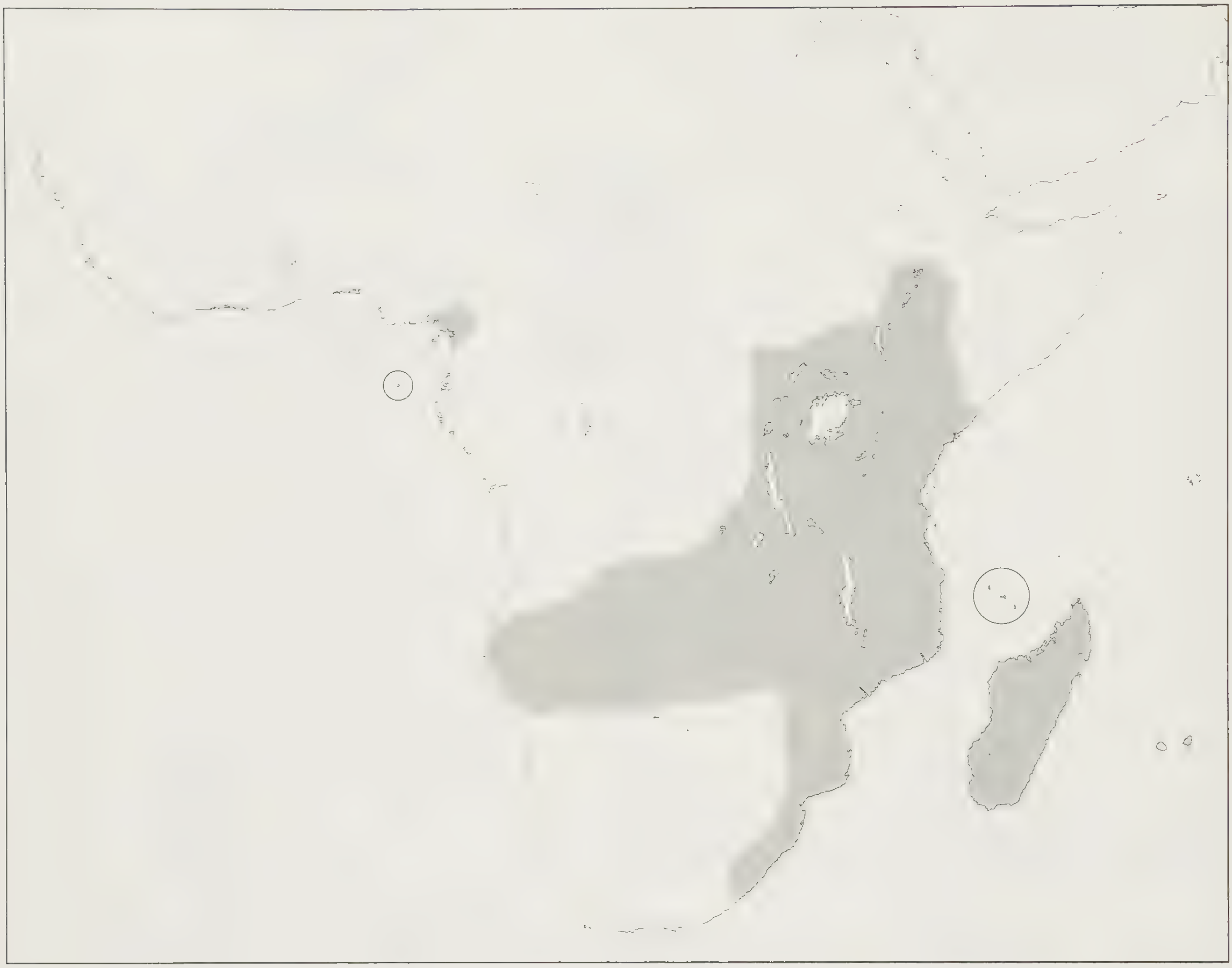

Fig. 70.2. Distribution map of *Cynorkis*.

Palynology

Pollen of *Cynorkis fastigiata* has hamulate sculpturing. The individual muri often coalesce with each other and enclose very small lumina (Schill and Pfeiffer 1977). **(AP)**

Cytogenetics

The only previously reported chromosome count for *Cynorkis anacamptoides* Kränzl. is $2n = 2x = 28$ (Thulin 1970). **(SD)**

Ecology

Most *Cynorkis* species are slender terrestrial herbs with fleshy or tuberous roots, but a few species are epiphytic. Examples include *C. kassneriana*, which occasionally grows at low levels on tree trunks and *C. synoensii*, which in addition to growing on moss-covered rocks can be found embedded in moss on lianas up to 5 m above the ground (la Croix and Cribb 1995). *Cynorkis* species usually grow in relatively wet habitats including marshes, swamps, bogs with sphagnum or tall grass, damp grassland, banks of watercourses, in crevices on seepage slopes, or on grass overlying rock slabs (Summerhayes 1968; Cribb and Stewart 1985; la Croix and Cribb 1995). Some species grow in leaf litter or on rotting logs in forests (e.g. *C. kassneriana*), in high rainfall *Brachystegia* (Fabaceae) woodland (e.g. *C. hanningtonii*) or in pine plantations (e.g. *C. buchanani* on the Zomba Plateau in Malawi), and sometimes in deep shade. *Cynorkis fastigiata* commonly grows in disturbed habitats in forests, on roadsides and in heathland, usually as individual plants (D. L. Roberts, personal communication). Members of the genus can form colonies (e.g. *C. anacamptoides*), and some species are common in certain localities. For example, several Malagasy species are frequently found in the high mountain forest vegetation and on rocky hill tops and granite outcrops in the centre of Madagascar (Nilsson *et al.* 1992). Others are less common, e.g. *C. compacta*, which is known from only a few localities in Natal, South Africa, where it occurs among rocks (Pridgeon 1992).

Most *Cynorkis* species grow at elevations of between 600–2300 m (la Croix and Cribb 1995) and up to 3000 m according to Summerhayes (1968). One exception is *C. kirkii*, which is reported to occur at 0–1800 m by la Croix and Cribb (1995) and 0–2400 m by Summerhayes (1968). The flowering period of *Cynorkis* can be prolonged as for *C. anacamptoides*, which flowers for almost six months between late September and mid-March, and fruits can be set rapidly at the base of an inflorescence still blooming at the apex (la Croix and Cribb 1995). According to Nilsson *et al.* (1992), reproductive success of *C. uniflora* on Madagascar is indirectly related to the presence of larval food plants (*Impatiens* [Balsaminaceae] and species of Apocynaceae) of the hawk-moth pollinators of this species. Some *Cynorkis* species are apomictic; *C. uncata* from east Africa reproduces asexually by means of axillary bulbils (Mabberley 1987). Under glasshouse conditions the robust Madagascan/Mascarenes species, *C. fastigiata*, readily sets fruit and disperses seeds, which germinate rapidly (Pridgeon 1992). **(RN)**

Uses

A few species, notably some of the showier Madagascan species, such as *C. gibbosa* Ridl., *C. uniflora* Lindl., and *C. lowiana* Rchb.f., are cultivated as pot plants. *Cynorkis* Kewensis is an artificial hybrid of *C. lowiana* and *C. fastigiata* Thouars. In Madagascar it is reportedly used to make pomades to treat burns (Kokwaro 1976) and *C. flexuosa* Lindl. is sometimes eaten in the east of the island (Usher 1974). **(PC)**

Cultivation

Many showy species with a history in cultivation including hybrids (e.g. *C.* Kewensis 1903). Composts A, B, C, or D depending on habitat. **(CB)**

Taxonomic notes

We have included the genus *Arnottia* within *Cynorkis*. It was distinguished by its non-resupinate flowers and solitary radical leaf. However, several *Cynorkis* have a similar vegetative morphology, although the flowers (apart the lip being uppermost) conform to those of other *Cynorkis* species. **(PC)**

Taxonomic literature

Perrier de la Bâthie, H. (1939). *Cynorkis*. In *Flore de Madagascar* I. (ed. H. Humbert), p. 74. Tananarive Imprimerie Officielle, Madagascar.

Szlachetko, D. L. and Olszewski, T. S. (1998). *Veyretella* Szlach. & Olsz. In *Flora Cameroun Orchidacées* (ed. B. Sabatie and P. Morat), **1**, 100.

71. DACTYLORHIZA

Dactylorhiza Neck. ex Nevski, *Act. Inst. Bot. Acad. Sc. U.R.S.S.*, ser. 1, **4**, 332 (1937). Type species: *Dactylorhiza umbrosa* (Kar. & Kir.) Nevski.

Coeloglossum Hartm., *Handb. Scand. Fl.*, 329 (1820). Type species: *Coeloglossum viride* (L.) Hartm.

Dactylorchis (Klinge) Verm., *Studies on Dactylorchids*, 64 (1947). Type species: *Dactylorhiza incarnata* (L.) Soó.

Derivation of name

From the Greek *dactylos*, finger, and *rhiza*, root, referring to the palmate tubers. **(JW)**

Description (Plates 90, 91; Fig. 71.1)

Small to large perennial *herbs*. *Rootstock* tuberous, tubers flat, palmately bifid or 5-fid, ovoid, oblong-cylindrical or cylindrical to napiform, often attenuated, rarely entire or shallowly bifid or trifid at apex, usually sessile. *Stem* erect or flexuose, solid or ± hollow, glabrous, leafy. *Leaves* basal, rosulate and/or cauline (most commonly cauline), often cucullate at apex, spotted purple, or unspotted. *Inflorescence* usually densely many-flowered; floral bracts leafy, rather fleshy, often exceeding the flowers. *Flowers* rose-purple, purplish violet, yellow, yellowish green, greenish brown or rarely white. *Sepals* glabrous. Dorsal sepal and *petals* often connivent and forming a loose hood. Lateral sepals usually free, rarely connivent, spreading or deflexed. *Labellum* entire and concave or ± three-lobed and flat, rarely elongate, spurred, surface flat, convex, undulate or deflexed, minutely papillose above, often with a darker coloured patterning of lines, loops or dots, ecallose, or with three basal calli, porrect to deflexed, sometimes linear-oblong and hanging vertically, spur cylindrical or conical, ± equalling ovary, or extremely short and obtuse with the entrance compressed by two transverse constrictions. *Column* short, erect; middle lobe of rostellum usually situated between parallel anther loculi; pollinia two, clavate, parallel, converging above or diverging, with caudicles, each adherent to a viscidium placed in a simple bursicle or viscidia virtually naked, the bursicle rudimentary. *Ovary* cylindrical-fusiform, sessile, twisted, glabrous. **(JW)**

Distribution (Fig. 71.2)

About 50 often poorly defined species occurring mostly in boreal, temperate, and less frequently, Mediterranean areas, from Iceland, northern Scandinavia and North Africa east to the Himalayas and Japan, as well as Madeira in the west to Siberia in the east and North America only in the Aleutian Islands. **(JW)**

Palynology

With minor variations among the 12 taxa examined (Schill and Pfeiffer 1977), the pollen surface of *Dactylorhiza* is laevigate-scabrate. In *D. elata* (Poir.) Soó and rarely in *D. maculata* (L.) Soó, *D. majalis* (Rchb.) P. F. Hunt & Summerh., and *D. traunsteineri* (Saut. ex Rchb.) Soó, the sculpturing is verrucose-hamulate, and also purely hamulate in *D. fuchsii* (Druce) Soó and *D. majalis*. Pollen of *D. viridis* (L.) R. M. Bateman, Pridgeon & M. W. Chase (cited as *Coeloglossum viride*) is reticulate with fragmented muri, distinctively different from other species. **(AP)**

Cytogenetics

With a basic number x = 20, *Dactylorhiza* comprises diploid ($2n = 2x = 40$) (Fig. C.2f) and polyploid ($2n = 4x = 80$ and $2n = 6x = 120$) species (Soó 1980*a*; Moore 1982). A chromosome number

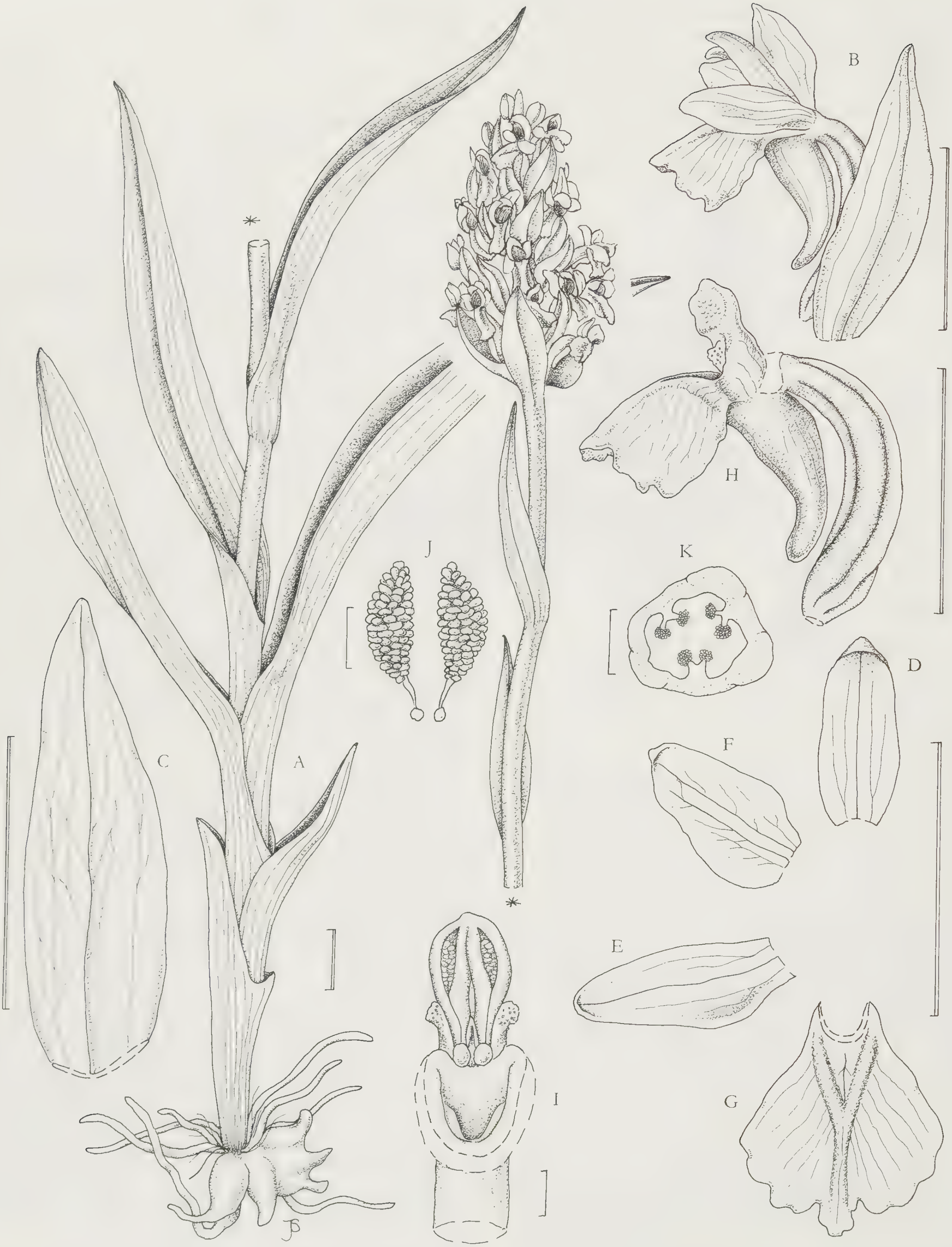

Fig. 71.1. *Dactylorhiza incarnata* (L.) Soó. A. Habit; B. Flower, side view; C. Bract; D. Dorsal sepal; E. Lateral sepal; F. Petal; G. Labellum; H. Labellum and column, side view; I. Column, front view; J. Pollinaria; K. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Lomax 669/7* (K) and Kew Spirit Collection no. 40634.

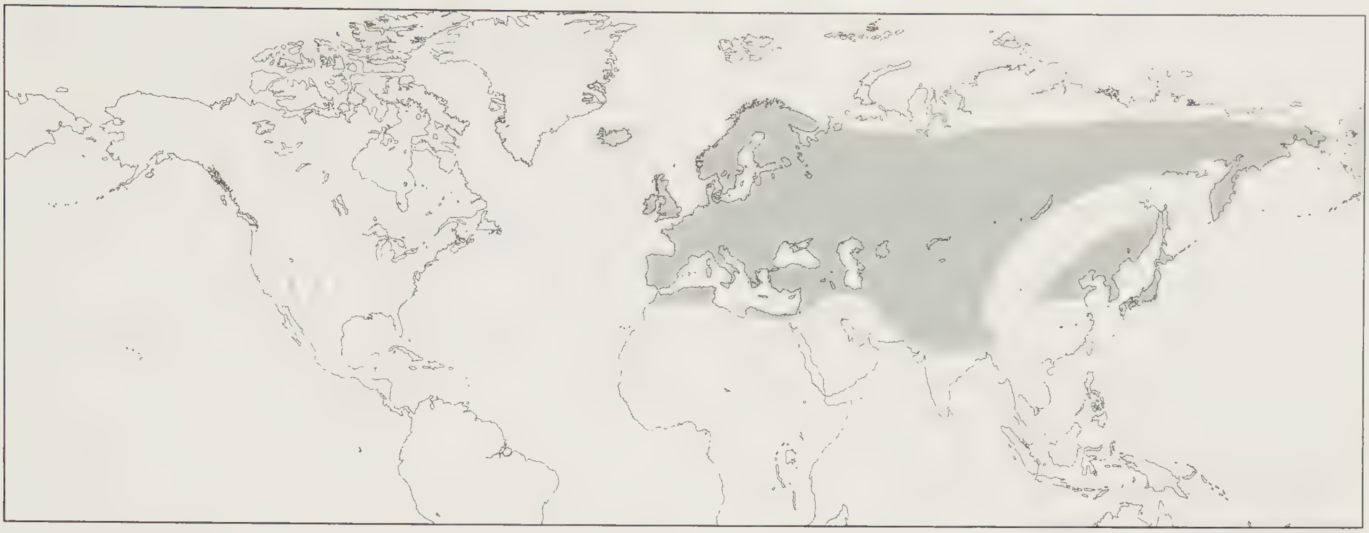

Fig. 71.2 Distribution map of *Dactylorhiza.*

with $2n = 3x = 60$ is known in *D. insularis* (Sommier & Martelli) Landwehr and *D. maculata* (L.) Soó subsp. *meyeri* (Rchb.f.) Tournay, although this is the typical number of hybrid taxa (Scrugli 1977; Vöth and Greilhuber 1980; D'Emerico *et al.* 1992). Cytological analysis of *D. romana* (Sebast.) Soó from southern Italy produced a chromosome number $2n = 40$, but some aneuploid individuals with $2n = 40 + 1$ B have been observed using C-banding (D'Emerico *et al.*, unpublished).

Chromosomes of *Dactylorhiza* are small, similar to those of *Neotinea* and *Orchis* groups with a somatic chromosome number of 42. Of the numerous species of *Dactylorhiza*, only *D. insularis* (D'Emerico *et al.* 1992), *D. maculata* subsp. *meyeri* (Vöth and Greilhuber 1980), and *D. romana* (D'Emerico *et al.*, unpublished) have been investigated karyologically. The C-banded chromosomes of some species of *Dactylorhiza* show centromeric heterochromatin and numerous chromosomes with telomeric heterochromatin. **(SD)**

Phytochemistry

Infection of the tubers of *D. sambucina* (cited as *O. latifolia* L.) and *D. viridis* (cited as *Coeloglossum viride*) with a strain of *Rhizoctonia repens* from *Orchis militaris* results in the synthesis of the phytoalexin orchinol (2,4-dimethoxy-7-hydroxy-9,10-dihydrophenanthrene) and *p*-hydroxybenzylalcohol. This observation was made as part of a survey of orchinol and *p*-hydroxybenzylalcohol production in a number of species representing genera in subtribe Orchidinae (Nüesch 1963; Gaumann *et al.* 1960).

The leaves of *D. fuchsii* and *D. viridis* contain kaempferol and quercetin. These flavonol aglycones were detected in acid-hydrolysed extracts of leaf tissue, indicating that they originate from flavonol *O*-glycosides (C. A.Williams 1979). Flavone *C*-glycosides were detected in *D. incarnata* and probably also occur in *D. praetermissa* (Williams 1979). Quercetin 3-*O*-β-D-glucoside (isoquercitrin) has been isolated from air-dried flowers of *D. sambucina* (Tira 1971). Further work by Pagani (1976) revealed the presence of quercetin 3-*O*-β-D-glucoside, quercetin 7-*O*-β-D-glucoside, and quercetin 3,7-di-*O*,*O*-β-D-glucoside in *D. sambucina.* This species also contains the phenylpropanoid esters caffeoyl-1-glucoside and *p*-coumaroyl-1-glucoside (Pagani 1976).

The anthocyanin content of the flowers of several *Dactylorhiza* species was investigated by Uphoff (1979). *Dactylorhiza maculata*, *D. majalis*, and *D. sambucina* contain cyanidin 3,5-diglucoside (cyanin) and the pigments orchicyanin I and II. Strack *et al.* (1989) analysed the anthocyanin content of 16 species of *Dactylorhiza* and also found cyanidin 3,7-diglucoside (seranin), ophrysanin, and serapianin in most of them. Orchicyanins I and II, ophrysanin, and serapianin were identified as cyanidin glucosides acylated with oxalic acid (Strack *et al.* 1986, 1989).

Baytop and Sezik (1968) reported on the chemical analysis of tubers of species collected in south-west Anatolia, Turkey. Their results were summarized in a later review by Ernst and Rodriguez (1984). The *Dactylorhiza* species analysed was *D. romana* (cited as *Orchis romana*). See *Anacamptis.* **(NV, RG)**

Ecology

The terrestrial orchid genus, *Dactylorhiza*, grows on a variety of soil types including both alkaline to acidic soils, although individual species sometimes show distinct pH preferences. For example, *D. fuchsii* usually grows on basic, calcareous soils, as seen with ssp. *hebridensis* (Wilmott) R. M. Bateman & Denholm in the alkaline 'machair' habitat of the Scottish Hebridean Islands. The closely related *D. maculata*, however, invariably grows on acidic substrates at a pH as low as 5.5, especially ssp. *ericetorum* (Linton) P. F. Hunt & Summerh. growing in the acidic heather moorland and peatbogs of Scotland. Of the other European *Dactylorhiza* species, many are typically found on alkaline to neutral soils, including *D. viridis*, *D. traunsteineri*, and *D. majalis* (Rchb.) P. F. Hunt & Summerh. subsp. *praetermissa* (Druce) D. M. Moore & Soó, although the Madeiran endemic, *D. foliosa* (Verm.) Soó, prefers acidic soils. According to

Delforge (1995), *D. incarnata* (L.) Soó subsp. *cruenta* (O. F. Müller) P. D. Sell grows on alkaline soils in the Alps but in quite acidic soils in Scandinavia (Summerhayes 1951; Lang 1989; Allan *et al.* 1993; Delforge 1995).

Dactylorhiza grows in full sun to semi-shade in a wide variety of often wet habitats, including grasslands and meadows, peat-bogs, marshes and fens, dune slacks, scrubland, and woodland (Summerhayes 1951; Lang 1989; Delforge 1995). Some individual *Dactylorhiza* species are tolerant of different soil moisture and light conditions. *Dactylorhiza maculata* in the north of Britain, for example, commonly grows on dry heaths and moors with *Erica* (Ericaceae) and *Molinia* (Poaceae) species and in slightly wetter areas with sphagnum moss, *Eriophorum* (*Cyperaceae*) species, and *Pinguicula* (Lentibulariaceae) (Lang 1989). Also, *D. fuchsii* in southern England grows on both open chalk downs and limestone grassland and in the more shaded habitat of oak, ash, and beech woodlands where it forms taller plants with larger inflorescences (Summerhayes 1951). Across the range of the genus, *Dactylorhiza* grows at a wide variety of elevations, from sea level in coastal sand dunes to montane environments at elevations up to 2500 m (Davies *et al.* 1988; Delforge 1995).

Flowering of *Dactylorhiza* usually takes place in the summer months, between May and July, although there are some earlier flowering species, such as *D. romana* from the Mediterranean, which starts flowering in March (Delforge 1995). For most species the rosette of leaves remains green throughout the flowering period and in some cases may not wither until the end of October (Möller 1987, cited in Rasmussen 1995). Exceptions are some plants such as *D. sambucina* (L.) Soó and *D. romana* growing in the Mediterranean region in which a 'wintergreen' rosette is formed that prevents desiccation in the dry summer. With the 'summer-green' species, the overwintering tuber develops over the spring and summer when the plant has fully expanded leaves. By the end of the year, the bud on the new tuber already contains the leaf and flower primordia for the next season (Harvais and Hadley 1967, cited in Rasmussen 1995). Replacement tubers of *D. fuchsii* in England can be seen at the base of the shoot in late November. Their growth rate increases in mid-April, reaching maximum size in September (Leeson *et al.* 1991).

Fruit-set levels ranging from an average of 10% (*D. sambucina* in Sweden and *D. viridis* in the Netherlands) to 39% (*D. fuchsii* in England) have been recorded from field populations of *Dactylorhiza* species (Neiland and Wilcock 1998; Willems and Melser 1998). Seed production varies from about 2000 to 5000 seeds per capsule (Salisbury 1942; Leeson *et al.* 1991; Neiland 1994; Willems and Mesler 1998) and, given an average of 17 capsules produced per *D. maculata* infloresence, Salisbury (1942) calculated that approximately 56 000 seeds could be produced per plant. Seeds are dispersed by the wind when the capsule dehisces at the end of the summer and germinate with a mycorrhizal fungus. The highest levels of seed germination are seen at a depth of 1–10 cm below ground level (van der Kinderen 1995). Germination of the seed takes place soon after dispersal (*D. fuchsii*; Leeson *et al.* 1991) or in the autumn when nutrition of the mycelium is optimal (*D. majalis*; Rasmussen and Rasmussen 1991). Several endophytes have been isolated from the roots of adult *Dactylorhiza* plants, which can stimulate seed germination or seedling growth *in vitro* (e.g. *Tulasnella calospora* is compatible with *D. majalis* and *Thanatephorus cumumeris* is compatible with *D. purpurella* (T. Stephenson & T. A. Stephenson) Soó; Hadley 1970; Rasmussen and Rasmussen 1991). Seeds may also be successfully germinated asymbiotically using nutrient media (e.g. Van Waes and Debergh 1986; Malmgren 1988) and even in water (Downie 1941; Vermeulen 1947). Following germination and formation of a protocorm, further seedling differentiation requires a period of cold temperatures, a factor which may restrict the geographic distribution at least of *D. majalis* (Rasmussen and Rasmussen 1991) and possibly other members of the genus.

Growth of the protocorm in many species may be quite rapid. For example, Leeson *et al.* (1991) observed that protocorms and small shoots were formed within three months after dispersing *D. fuchsii* seed in the field and under symbiotic cultural conditions. After 8–10 months in culture, small plants had developed that had a single tuber, two leaves, and several roots. Rapid development from germination to shoot and tuber formation is also reported for *D. sambucina* (Fuchs and Ziegenspeck 1927), but Rasmussen (1995) suggested that longer lengths of up to four years for other members of the genus may be overestimates. It has been thought to take several more years for *Dactylorhiza* plants to reach maturity and produce an inflorescence, e.g. 4–5 years in *D. fuchsii* and *D. incarnata* (Wells 1981) or 16 years according to Ziegenspeck's estimates (cited in Rasmussen 1995) for *D. majalis* and *D. incarnata.* But a number of other studies have shown that the length of time for the development from seed to flowering individual in *Dactylorhiza* species can be relatively short, e.g. 2–3 years in *D. praetermissa* (Vermeulen 1947), 2.5–3.5 years in *D. majalis* (Sipkes 1967, 1968, cited in Vanhecke 1991), three years in *D. praetermissa* (McKendrick 1995), and 24–27 months for a range of *Dactylorhiza* species (Möller 1987). In the short-lived species, *Dactylorhiza viridis* (half-life *c.* 1.5 years) plants are able to produce an inflorescence the first time they emerge above ground (Willems and Melser 1998). In other species with longer lifespans, flowering may be delayed until the plants reach a certain size. In *D. praetermissa*, for example, symbiotically propagated plants may produce leaf rosettes for several years before flowering takes place (McKendrick 1995). The probability of flowering has been shown to be related to leaf number in *D. fuchsii*, with plants having four or fewer leaves unlikely to flower and those with ten or more leaves more likely to flower (Leeson *et al.* 1991).

The frequency of flowering in populations of *Dactylorhiza* can be quite high, although it is also variable. In Tamm's long-term demographic study in Sweden (1943–1990), the frequency of flowering of a population of *D. sambucina* varied from 0–86% (Tamm 1991), whereas in the study by Vanhecke *et al.* (1991) of *D. praetermissa* in Belgium flowering varied from 16%–69%, with about 50% of plants flowering in most years. Similarly, the mean flowering of a population of *D. viridis* in the Netherlands was also 50% (Willems and Melser 1998). The variation in flowering frequency may be partially explained by climatic variables such as precipitation (Tamm

1991), whereby summer drought negatively affects the following year's flowering (Inghe and Tamm 1988), but, at least in *D. sambucina*, there is also a tendency for flowering plants to remain vegetative the next year (Inghe and Tamm 1988). Dormancy occurs rarely in *D. viridis* and lasts only for one season when it does take place (Willems and Melser 1998) but presumably can occur more frequently in long-lived members of the genus. Some *Dactylorhiza* species are notably long-lived (e.g. *D. sambucina*, Tamm 1948; *D. fuchsii*, Summerhayes 1951) and can form clumps of plants due to vegetative multiplication of the tubers. Perennation by means of tubers has been used to explain the persistence of some *Dactylorhiza* populations where recruitment from seed has been low and irregular (e.g. populations of *D. sambucina* and *D. incarnata* in Sweden; Tamm 1991). In *D. viridis*, however, vegetative propagation is insignificant, and instead population persistence depends on regular recruitment from seed (Summerhayes 1951; Willems and Melser 1998). Where recruitment in *Dactylorhiza* is high, large populations of several thousand plants can form (Vanhecke 1991) with diverse age structures (Willems and Melser 1998). High seed input can also allow *Dactylorhiza* species to re-invade sites from which they have disappeared (e.g. *D. praetermissa* lost from coastal sites near Zeebrugge in Belgium due to flooding; Vanhecke 1991) or to colonize new habitats (such as *D. praetermissa* and *D. purpurella* colonizing artificial calcareous substrates left by industrial activity near Manchester in England; Adcock *et al.* 1983). Absence of seed recruitment eventually leads to population decline (Tamm 1991) with rare species being particularly threatened by absence of fruit-set, such as *D. lapponica* (Laest. ex Rchb.f.) Soó (Neiland and Wilcock 1993, 1998).

Among the members of the genus are a number of species that are either rare and/or declining. The relatively common, widespread species, *D. viridis*, has declined from 55 known populations in the Netherlands before 1950 to just two known sites today (Willems and Melser 1998), and the scarce *D. traunsteineri* has decreasing numbers of populations throughout its European range. *Dactylorhiza foliosa* has a restricted distribution (on Madeira) and is collected for horticulture (Delforge, cited in IUCN Orchid Specialist Group 1996). Habitat change caused by changes in agricultural practices, land drainage, or soil fertilization is a major threat to the continued survival of many *Dactylorhiza* populations. For example, alterations in light levels caused by the invasion of trees and other tall plants into old herb-rich meadows in Scandinavia, in which traditional hay-making practices have ceased, has caused a decline in shade-intolerant species such as *D. sambucina* in these habitats (Norderhaug *et al.* 1997). Drainage of nutrient-rich mires for forestry threatens wetland species such as *D. incarnata* (Kuitenen and Kuitenen 1994). Fertilizers are frequently used to 'improve' grasslands in which *Dactylorhiza* species occur; but these have been shown to have negative effects on the growth of *D. majalis* and *D. fuchsii* (Dijk and Olff 1994; McKendrick 1996) and to increase competition with co-occuring plants. Conservation of threatened *Dactylorhiza* populations can be achieved by careful management of sites (such as mowing, selective grazing, and reducing fertilizer applications) to maintain optimum environmental conditions and allow for adequate recruitment of seeds to replenish the population (Willems and Melser 1998). **(RN)**

Pollination

Dactylorhiza viridis is the only species that provides nectar in a short spur (van der Pijl and Dodson 1966). Insects reported to carry pollinaria include saw-flies, wasps, bees, and beetles (van der Cingel 1995; van der Pijl and Dodson 1966). The remaining species of *Dactylorhiza* lack nectar in their spurs and attract pollinators by deceit (Dafni 1987). The principal pollinators seem to be queen bumble-bees, such as in *D. sambucina* (Nilsson 1980). After emergence from hibernation, inexperienced queens are deceived by the large, brightly coloured flowers, which they mistakenly consider to be a food source. Learning avoidance of the orchids may be reduced due to the presence of two colour morphs (Ferdy *et al.* 1998; Smithson and Macnair 1997). Other species of *Dactylorhiza*, such as the diploid *D. fuchsii* and the tetraploid *D. maculata*, are also visited by Diptera and especially Coleoptera. Longhorn beetles (Cerambycidae) have repeatedly been reported to visit and pollinate *D. fuchsii* and *D. maculata* (Reinhard *et al.* 1991; Vöth 1983). These beetles seem to feed on papillae on the labellum and in the spur (Vöth 1983). An extraordinary phenomenon was observed by Dafni and Woodell (1986) in populations of *D. fuchsii* from England. They found that honey-bees are able to exploit a glucose-rich stigmatic exudate, whereas bumble-bees cannot exploit this resource. The presence of hybrid swarms between *Dactylorhiza* species further indicates that pollinators are not specific. **(AW, SC, AD)**

Uses

Dactylorhiza plants are increasingly grown as garden or pot plants in Europe. Some of the hybrids are particularly vigorous. **(PC)**

Cultivation

Dactylorhiza is one of the most successful cultivated genera of Orchideae. Garden-worthy species include *D. elata*, *D. praetermissa*, and *D. fuchsii*, the latter a good candidate for naturalizing. Some species hybridize freely, giving rise to superior forms, which may be polyploid. Plants are found in marshy areas, grassland, and woodland, on acid and alkaline soils according to species. Most will grow well in containers in compost C and D and some in artificial bogs. **(CB)**

Taxonomic notes

This is a taxonomically notorious critical genus that, like *Ophrys*, has received much attention in recent years. Taxa are either diploid or tetraploid, the latter including both auto- and allotetraploids. The diploid taxa are distinct in most cases but the tetraploids less so, intergrading into each other in many cases. Species often occur in large populations, often in marshy habitats, where they can breed freely. In addition, some of the mechanisms of reproductive isolation appear to be reduced or ineffective, and confusing transitional forms occur in areas where taxa are sympatric. Variation is so great and hybrid swarms so large that they often exceed the numbers of pure parents in a population. The interpretation of otherwise distinct taxa becomes difficult in such areas.

The genus appears well adapted to diverse ecological conditions, often through extensive hybridization in disturbed habitats. It is clear that there is still no consensus of opinion on the systematics of *Dactylorhiza*, and the number of taxa and their nomenclature remains open to debate.

Molecular analyses (Bateman *et al.* 1997) indicated that *Dactylorhiza* is paraphyletic and that *Coeloglossum* nests within *Dactylorhiza*. Although *Coeloglossum* is the earlier name, it is monospecific, and a proposal to conserve *Dactylorhiza* over *Coeloglossum* is in press but has yet to be accepted. **(JW)**

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72. DIPHYLAX

Diphylax Hook.f. in Hook., *Icon. Pl.*, **19**, t. 1865 (1889); Kränzl., *Orch. Gen. Sp.*, **1**, 598 (1901). Type species: *Diphylax urceolata* Hook.f.

Habenaria sect. *Diphylax* (Hook.f.) Hook.f., *Fl. Brit. India*, **6**, 165 (1890).

Habenaria sect. *Dithrix* Hook.f., *Icon. Pl.*, **19**, t. 1865 (1889); Type species: *D. decipiens* Hook.f.

Tsaiorchis T. Tang & F. T. Wang, *Bull. Fan Mem. Inst. Biol. Bot.*, **7**, 131 (1936), **synon. nov.** Type species: *T. neottianthoides* T. Tang & F. T. Wang.

Derivation of name

From the Greek *di*, two or double, and *phylax*, a guard, in allusion to the two slender staminodes (lateral appendages) on each side of the anther. **(PC)**

Description (Fig. 72.1)

Small, terrestrial *herbs* growing from oblong-ovoid tubers. *Leaves* suberect, 1–3, subradical, rather fleshy. *Inflorescence* terminal, subdensely few- to many-flowered, secund; bracts ovate to lanceolate. *Flowers* small, white and pink or purple sometimes with green. *Sepals* free, not spreading widely. *Petals* similar, one-nerved. *Labellum* entire to distally three-lobed, spurred at the base, ecallose, sometimes puberulous. *Column* small; anther loculi parallel, closely spaced, canals short; pollinia two, clavate, with short caudicles and two relatively large viscidia; lateral appendages elongate, capillary, clavate or tapering at the apex; stigma confluent or bipartite, sessile. *Ovary* with a short pedicel. **(PC)**

Distribution (Fig. 72.2)

A small genus of three or four species ranging from the Himalayas to southern China. **(PC)**

Ecology

Members of the Asian genus *Diphyllax* are terrestrial plants and grow at high elevations. *Diphylax urceolata* was recorded at 3300–4200 m in the Himalayas (Hara *et al.* 1978). **(RN)**

Uses

None recorded. **(PC)**

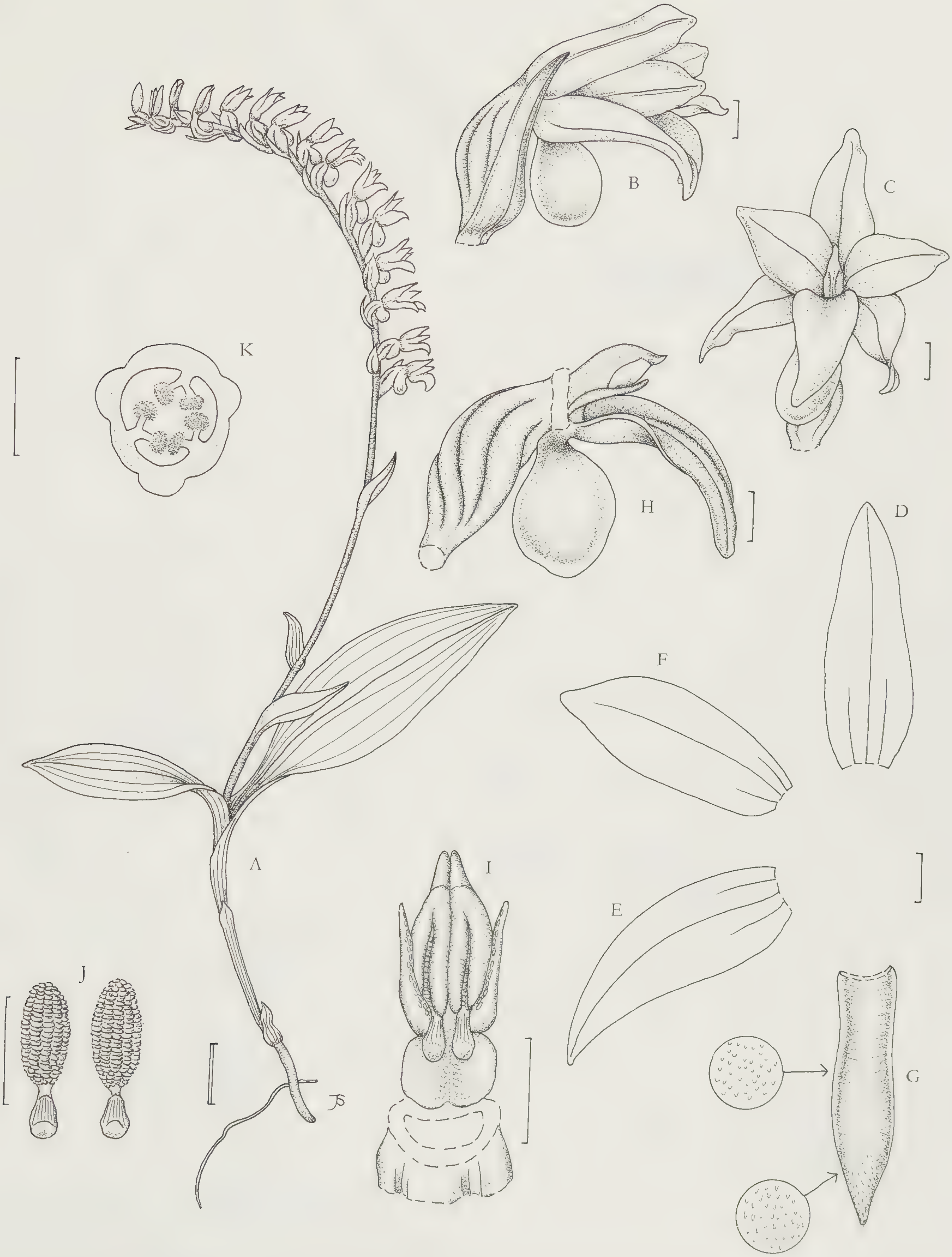

Fig. 72.1. *Diphylax urceolata* Hook.f. A. Habit; B. Flower, side view; C. Flower, front view. D. Dorsal sepal; E. Lateral sepal; F. Petal; G. Labellum; H. Labellum and column, side view; I. Column, front view; J. Pollinaria; K. Ovary, transection. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Kingdon Ward 8650* and *Kingdon Ward 8544*.

Fig. 72.2. Distribution map of *Diphylax.*

Cultivation

Compost C. **(CB)**

Taxonomic notes

The small flowers of these plants have made it difficult to ascertain the structure of their columns. Hooker f. (1890) noted that he had dissected many herbarium specimens before detecting the capillary lateral appendages (which he termed staminodia). Tang and Wang noted the similarity of their new genus *Tsaiorchis* to *Diphylax* but distinguished it on its remarkable rostellum, which is canaliculate, projecting beyond the column and bifid, the lower part being entirely united to the gynostemium. The viscidia of *T. neottianthoides* are hidden in the cavity formed by the lip and gynostemium. The rostellum of *D. urceolata* is far less well developed. However, we consider these taxa to be close enough to unite them in a single genus. **(PC)**

Taxonomic literature

Hooker, J. D. (1890). *The flora of British India* 6. *Orchideae.* Reeve, London.

73. DIPLOMERIS

Diplomeris D. Don, *Prodr. Fl. Nepal.*, 26 (1825); Benth. & Hook.f., *Gen. Pl.*, **3**, 627 (1883). Type species: *D. pulchella* D. Don

Diplochilus Lindl., *Bot. Reg.* sub t., 1499 (18). Type species not designated.

Paragnathis Spreng., *Syst. Veg.*, 3, 675 (18). Type species: *P. pulchellus* Spreng.

Derivation of name

From the Greek *diplous*, double, and *meris*, a portion, descriptive of the two arms to the column. **(PC)**

Description (Plate 92; Fig. 73.1)

Small, deciduous, terrestrial *herbs* growing from globose tubers. *Leaves* 1–3, radical, suberect, oblong to ovate-lanceolate, glabrous, green. *Inflorescence* arching or spreading, suberect, 1–2-flowered; peduncle slender, pubescent; bracts lanceolate, green. *Flowers* large, white. *Sepals* free, spreading, subsimilar, glandular. *Petals* large, spreading, entire, much broader than the sepals, glabrous. *Labellum* pendent, sessile, flabellate, shortly apiculate, glabrous, spurred at the base, ecallose; spur slenderly cylindric, decurved. *Column* short; anther loculi short; parallel; pollinia two, clavate; lateral appendages two, sessile; stigmatic lobes oblong, more or less connate; rostellum broad, membraneous, side lobes slender, elongate. *Ovary* and pedicel glandular. **(PC)**

Distribution (Fig. 73.2)

Two species in the Himalayas of Nepal, Bhutan, India, northern Vietnam, and southern China. **(PC)**

Cytogenetics

Diplomeris hirsuta D. Don, with $2n = 2x = 42$ chromosomes, is based on $x = 21$ (Mehra and Kashyap 1976). **(SD)**

Ecology

Members of the Asian genus *Diplomeris* are terrestrial herbs that can grow at relatively high elevations, for example, at locations in the Himalayas. Hooker (1894) recorded that *D. pulchella* grew in the Khasia Hills in India at 1200–1500 m and that *D. hirsuta* grew in Nepal and western Bhutan at 450 m. *Diplomeris pulchella* may spread vegetatively. Hooker (1894) described it as having a 'creeping rootstock'. It is rare in at least some parts of its range. For example, it

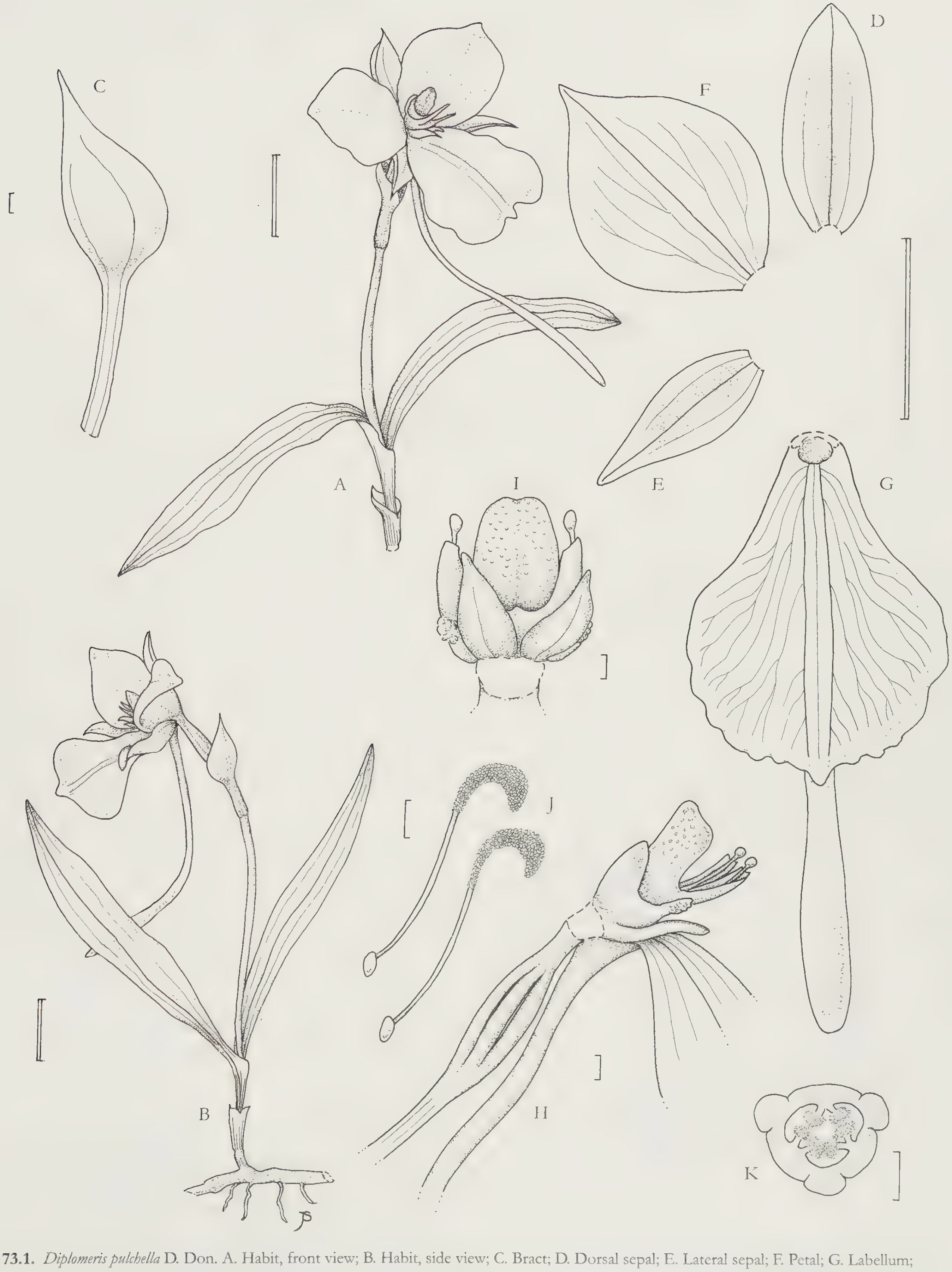

Fig. 73.1. *Diplomeris pulchella* D. Don. A. Habit, front view; B. Habit, side view; C. Bract; D. Dorsal sepal; E. Lateral sepal; F. Petal; G. Labellum; H. Labellum (portion) and column, side view; I. Column, front view; J. Pollinaria; K. Ovary, transection. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *J.D.A.T.I.J. L-256* (Herbarium Hookerianum 1867).

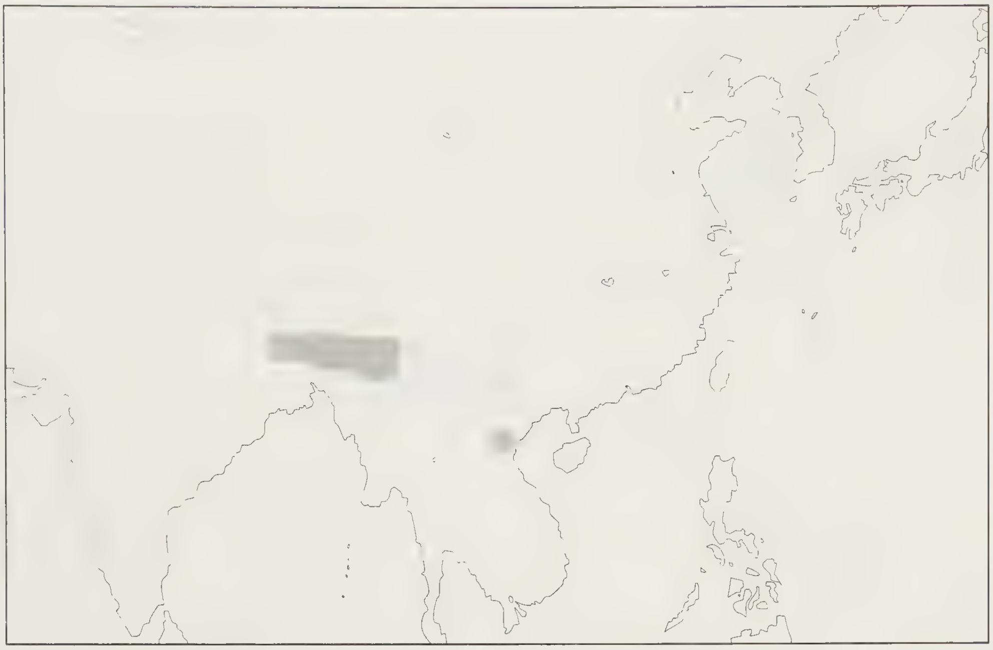

Fig. 73.2. Distribution map of *Diplomeris.*

was listed as one of the rare species at the proposed Namdapha Biosphere Reserve in Arunachal Pradesh, India, along with some other orchids (Kulshrestha and Shukla 1987). **(RN)**

Uses

Occasionally grown for its showy flowers. **(PC)**

Cultivation

Diplomeris have a dormant period that they survive as tubers. These can be planted 1 cm deep in a mix of 1 part chopped sphagnum moss, 2 parts sterilized loam, 1 part polystyrene granules, or 1 part peat or in a mix of 4 parts fibrous loam, 1 part chopped, sterilized leaf mould, 1 part washed sand, 1 part finely chopped sphagnum. The pan should be placed in half shade and watered by soaking regularly from May onward through the growing season. After flowering, the watering can be reduced until the leaves wither. **(PC)**

74. DRACOMONTICOLA

Dracomonticola H. P. Linder & Kurzweil, *Willdenowia*, **25**, 229 (1995). Type species: *Dracomonticola virginea* (Bolus) H. P. Linder & Kurzweil. [*Platanthera virginea* Bolus, *Ic. Orch. Austr.-afr. Extratrop. 1*, t. 60 (1896)].

Derivation of name

From the Latin *draco*, dragon, *mons*, *montis*, mountain, and the suffix *-cola*, inhabitant, referring to the Drakensberg in KwaZulu-Natal (South Africa), where the sole species of this genus occurs. **(HK, PL)**

Description (Fig. 74.1)

Slender *herbs* with testicular tubers, growing more or less horizontally out of rock crevasses in cliffs. *Leaves*: basal leaf solitary, ovate-lanceolate, acute; much smaller cauline leaf usually present. *Inflorescence* a head-like cluster with few flowers, somewhat nodding; bracts green, slightly longer than the ovaries, acute. *Sepals* subequal, elliptic, acute, somewhat concave. *Petals* free from the column, less than half as long as the sepals, ovate, obtuse, folded over the column, concave. *Labellum* pandurate, with shallowly concave hypochile with a callus and flat triangular epichile with minute side lobes. *Column* with the anther reflexed at an angle of approximately 45°, thecae two, parallel and adjacent; pollinia sectile, viscidia two; lateral appendages small; rostellum three-lobed with small central lobe between the thecae, with globose, ebursiculate viscidia; stigma shallowly concave, with an entire or bilobed process. **(HK, PL)**

Distribution (Fig. 74.2)

A monospecific genus, widespread in the Drakensberg in KwaZulu-Natal (South Africa) and Lesotho. **(HK, PL)**

Phylogenetics

The sole species of this genus was originally described in the genus *Platanthera* by Bolus (1896), who pointed out its peculiar nature. Later it was treated as an 'anomalous' *Brachycorythis* species by Rolfe (1912–1913). Without giving exact reasons Schlechter (1915) transferred it to *Neobolusia*, which was also accepted by Schelpe (1966) and Stewart *et al.* (1982). In a comparative study of the southern African Orchidinae Kurzweil and Weber (1991) pointed out that the species is different from the other *Neobolusia* species and apparently incorrectly placed there. It was later segregated as the mono-

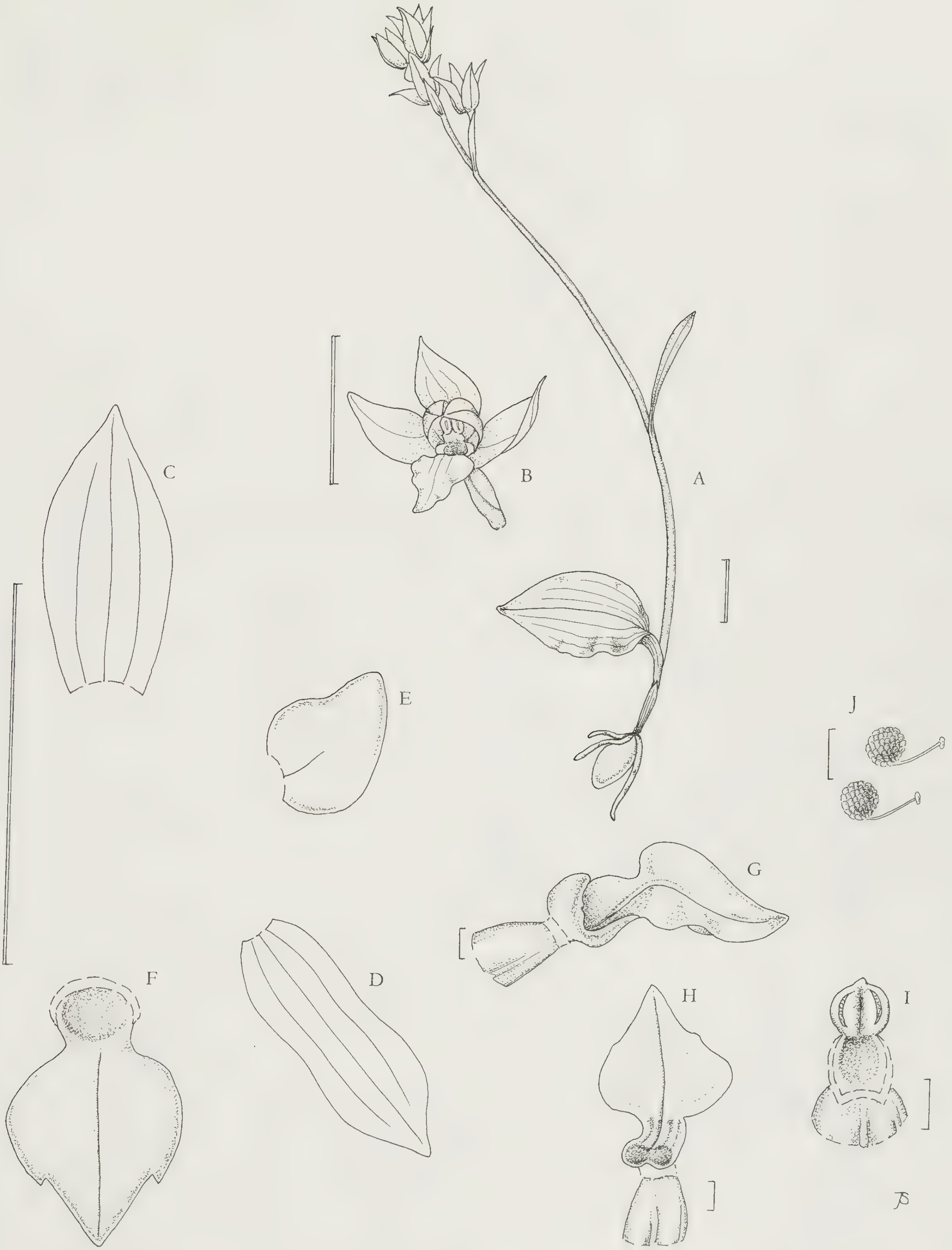

Fig. 74.1. *Dracomonticola virginea* (Bolus) H. P. Linder & Kurzweil. A. Habit; B. Flower; C. Dorsal sepal; D. Lateral sepal; E. Petal; F. Labellum from above; G. Labellun and column from side; H. Labellum from below; I. Column from front; J. Pollinaria. Single bar = 1 mm, double bar = 1 cm. Habit and flower redrawn by Judi Stone from a figure by Claire Linder (neé Smith) from Linder and Kurzweil (1999), *Orchids of Southern Africa,* A. A. Balkema, Rotterdam. Dissections redrawn by Judi Stone from Bolus, *Ic. Orch. Austr.-afr. Extratrop. 1*, t. 60 (1896).

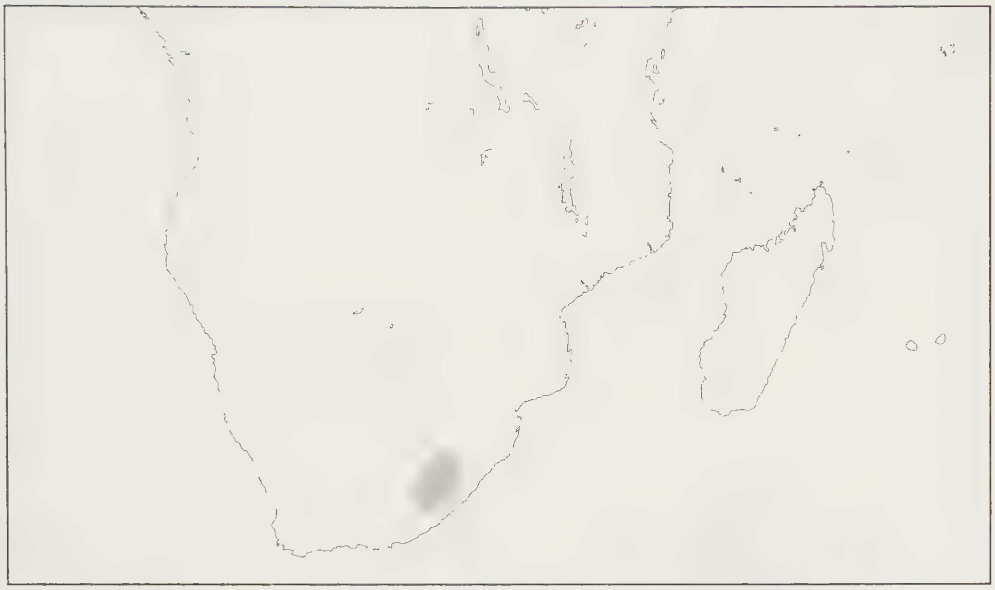

Fig. 74.2. Distribution map of *Dracomonticola.*

specific genus *Dracomonticola* (Linder and Kurzweil 1995). Differences from *Neobolusia* are the unusual habit with the ovate basal leaf, the short petals, the lack of the fusion between petals and column, the stigma process, and the reflexed anther (Bolus 1893–1896; Kurzweil and Weber 1991; Linder and Kurzweil 1995). On the basis of the unusual column architecture with its reflexed anther and the stigma process, *Dracomonticola* was considered phylogenetically isolated (Linder and Kurzweil 1995).

The spreading sepals, the short petals, the nodding inflorescence, and the minute lateral lobes of the lip indicate a close relationship to *Schizochilus* (Kurzweil and Weber 1991; Linder and Kurzweil 1995). In addition, the pandurate lip with its shallowly concave hypochile and laminal callus is similar to that found in *Schizochilus.* However, the short or minute lip spurs that characterize *Schizochilus* are absent in *Dracomonticola.* Alternatively, the saccate lip might also indicate an affinity to the *Brachycorythis-Neobolusia* group as reflected in the taxonomic literature (Schelpe 1966; Stewart *et al.* 1982). **(HK, PL)**

Ecology

Dracomonticola virginea is generally found above 2500 m. It tends to occur on south-facing rock ledges on basalt, forming cool, shady habitats. The plants are frequently common or densely clustered in these habitats. Flowering time is early summer. **(HK, PL)**

Uses

None recorded. **(HK, PL)**

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75. GALEARIS

Galearis Raf., *Herb. Raf.*, 71 (1833); *Fl. Tellur.* **2**, 39 (1836). Type species: *Galearis spectabilis* (L.) Raf.

Galeorchis Rydb., in Britton, *Man. Fl. N. U.S.*, 292 (1901). Type species: *Galearis spectabilis* (L.) Raf.

Aorchis Verm., *Jahresb. Naturwiss. Ver. Wuppertal.*, 25, 32 (1972). Type species: *Aorchis spathulata* (Lindl.) Verm.

Derivation of name

From the Latin *galea*, a helmet, in reference to the hood covering the column created by the connivent sepals and petals. **(JW)**

Description (Plate 93; Fig. 75.1)

Small to medium-sized *herbs. Rootstock* fibrous to fleshy, borne from a very short rhizome. *Stem* scapose, glabrous. *Leaves* one or two, basal, suborbicular to broadly elliptic, obtuse, fleshy, unspotted. *Inflorescence* a lax, up to 15-flowered raceme; floral bracts leafy, conspicuous, narrowly elliptic, acute. *Flowers* showy. *Sepals* and *petals*

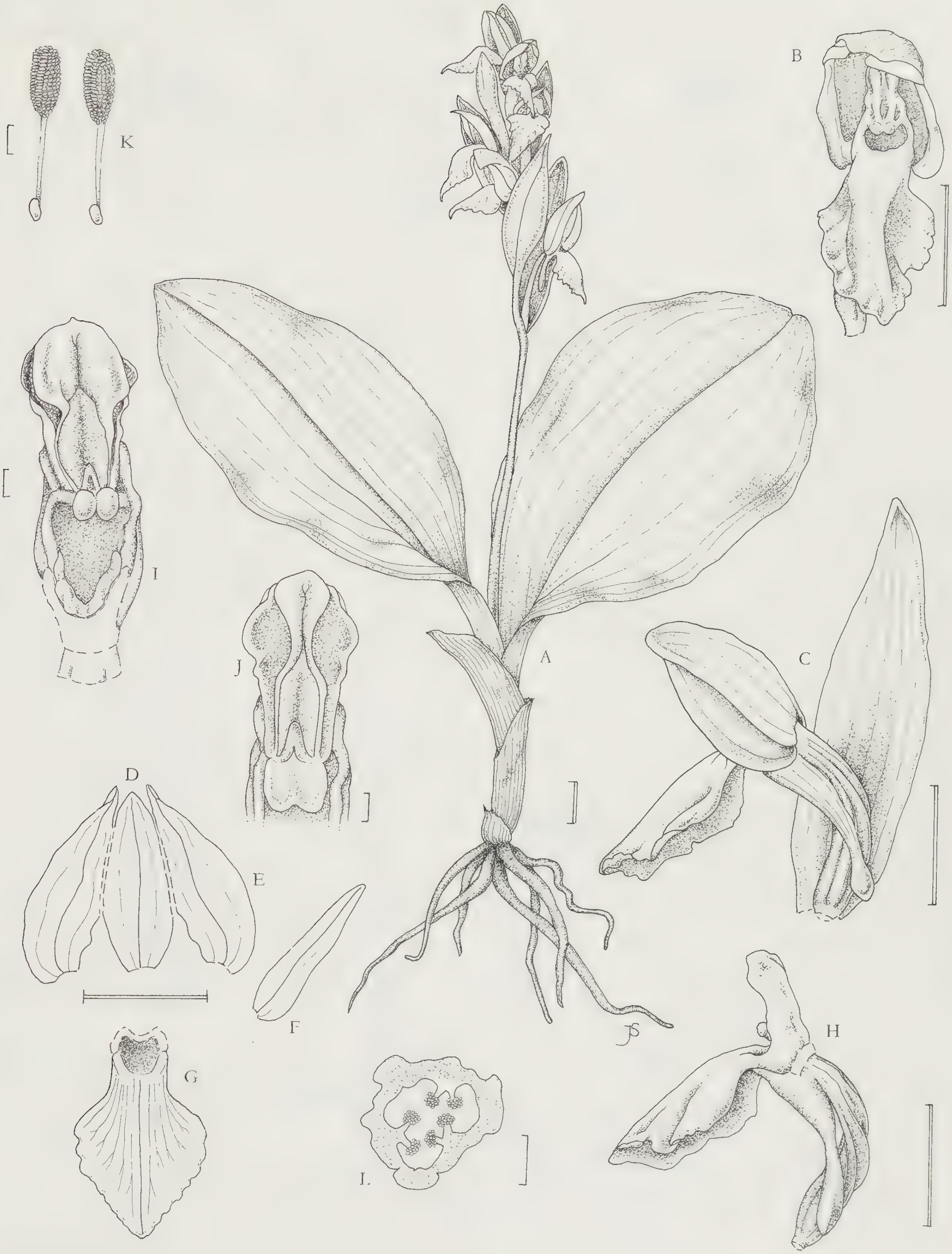

Fig. 75.1. *Galearis spectabilis* (L.) Raf. A. Habit; B. Flower, front view; C. Flower and bract, side view; D. Dorsal sepal; E. Lateral sepal; F. Petal; G. Labellum; H. Labellum, column, and ovary, side view; I. Column, front view; J. Column (pollinaria removed); K. Pollinaria; L. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Pringle 3/78* and Kew Spirit Collection no. 45326.

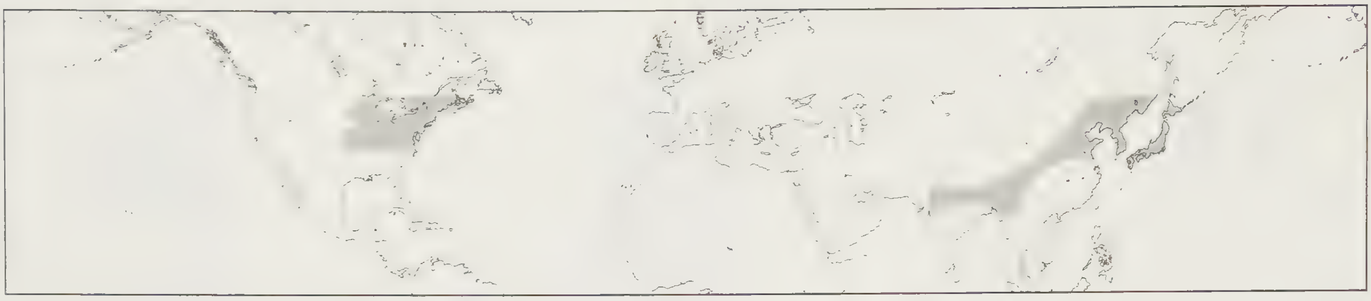

Fig. 75.2. Distribution map of *Galearis.*

purplish or lilac-pink, lip white or pale pink, sometimes entirely white. Dorsal and lateral sepals connivent with petals, forming a hood over column, glabrous. *Labellum* entire or rarely obscurely three-lobed, spurred, broadly rhomboid-cuneate, elliptic or ovate, obtuse, margins undulate, spur stout. *Column* short, stout; anther loculi separate; pollinia two, each with a caudicle and viscidium, which are enclosed in a solitary bilobed bursicle situated above the stigma and nectary orifice or attached to a solitary viscidium enclosed in a bursicle. **(JW)**

Distribution (Fig. 75.2)

Three to perhaps six species distributed in China, Japan, the Himalayan region, and North America. **(JW)**

Ecology

Members of the genus *Galearis* are terrestrial orchids with rhizomes and fleshy roots (Hunt 1971). They can grow at high elevations, as seen with Himalayan members of the genus, e.g. *G. stracheyi* (Hook.f.) P. F. Hunt grows at 3600–4800 m in the Himalayas (Garhwal to Bhutan) and *G. spathulata* (Lindl.) P. F. Hunt at 3300–5000 m in the Himalayas and Tibet (Hara *et al.* 1978). In the USA, *G. spectabilis* is an inhabitant of damp, deciduous forests and is a 'summer-green' species, its leaves appearing in May and not withering until the autumn. The underground storage organs develop simultaneously with the foliage leaves and reach full size in the late autumn when the leaves and old roots are senescing (Rasmussen 1995). Seeds dispersed by *G. spectabilis* following fruit-set in the autumn can remain viable in the soil for over six months as demonstrated in experimental sowing trials performed in the field in Maryland, USA, when seeds sown in November started to germinate in the following June (Rasmussen and Whigham 1993). *Galearis spectabilis* seedlings start to form mycorrhiza about 21 weeks after germination begins. The subsequent mycorrhizomes are long and slender in shape, usually with small, lateral shoots, and it is from these that the first leafy shoots and underground storage organs are produced in the spring (Rasmussen 1995). **(RN)**

Uses

None recorded. **(JW)**

Cultivation

Little is known about growing *Galearis. Galearis spectabilis* from North America may be grown in compost D. **(CB)**

Taxonomic notes

The non-tuberous rootstock and the one or two basal leaves preclude inclusion in *Orchis s.s.* as originally proposed for the familiar *G. spectabilis* by Linnaeus. Rydberg (1901) proposed changing *Galearis* to *Galeorchis* fearing confusion with the genus *Galearia* (Pandaceae). This proposal was rejected in 1968 by the International Association for Plant Taxonomy Committee, which officially conserved *Galearis* over *Galeorchis.* We follow Hunt (1971) in including Asiatic species subsequently referred to *Aorchis* by Vermeulen (1972) within this genus. **(JW)**

Taxonomic literature

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76. GENNARIA

Gennaria Parl., *Fl. Ital.*, **3**, 404 (1858). Type species: *G. diphylla* (Link) Parl.

Derivation of name

Named in honour of Bennedetto Gennari, an Italian painter of the 17th century. **(PC)**

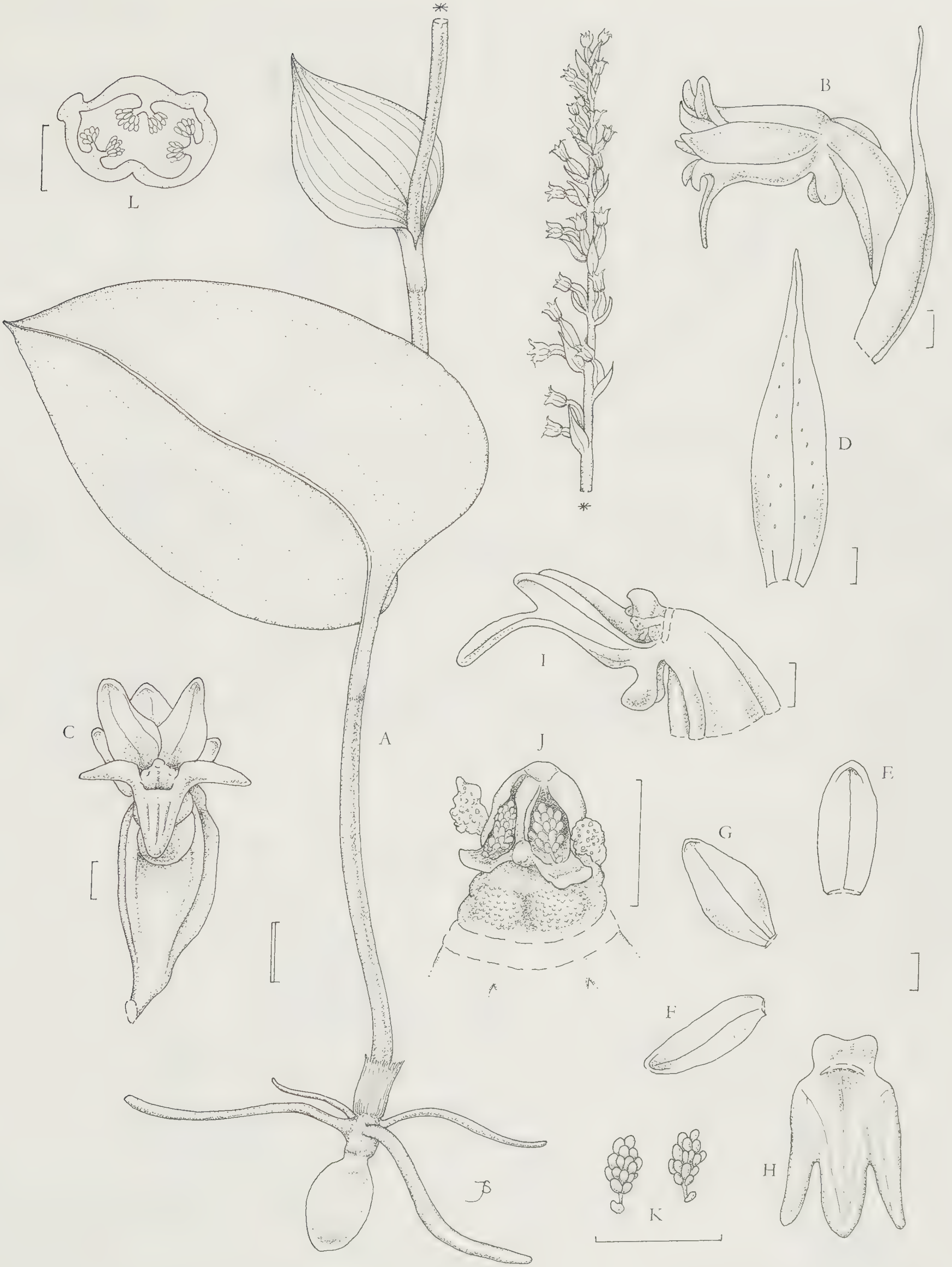

Fig. 76.1. *Gennaria diphylla* Parl. A. Habit; B. Flower, side view; C. Flower, front view; D. Bract; E. Dorsal sepal; F. Lateral sepal; G. Petal; H. Labellum; I. Labellum, spur, and column, side view; J. Column, front view; K. Pollinaria; L. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from Herbarium Churchillianum Proprium no. 249 (K) and Kew Spirit Collection no. 43749.

Description (Plate 94; Fig. 76.1)

A small to medium-sized terrestrial *herb* growing from a large ellipsoidal tuber, further tubers produced on stolons. *Stem* erect, with 1–2 basal sheaths and 1–2 alternate leaves. *Leaves* spreading cordate, sheathing at base, glossy, green. *Inflorescence* erect to slightly arcuate, subsecund, densely many-flowered; bracts small, ovate-lanceolate, acuminate, green. *Flowers* small, sub-campanulate with only the tips of the perianth spreading, yellow-green. *Dorsal sepal* oblong, obtuse. *Lateral sepals* similar but oblique. *Petals* longer and broader, slightly fleshy at tips. *Labellum* three-lobed in apical half, somewhat decurved, spurred at the base; spur saccate, short. *Column* short; anther bilocular, the locules divergent at base; pollinia pyriform, with small caudicles; viscidia two, small, suborbicular, imperfectly concealed by the inflexed tips of the stigmatic canals; lateral appendages two, stalked, as long a the column; stigma bilobed, convex, connate just below summit; rostellum small, triangular. *Ovary* fusiform, twisted, only shortly pedicellate. **(PC)**

Distribution (Fig. 76.2)

The single species, *G. diphylla*, is found in Corsica, Sardinia, Algeria, Morocco, southern Spain, Portugal, Madeira, and the Canary Islands (Porto Santo, Tenerife). **(PC)**

Cytogenetics

The genus *Gennaria* is based on x = 17; *G. diphylla* (Link) Parl. has $2n = 2x = 34$ chromosomes (Scrugli 1978; Sundermann and von der Bank 1977). However, $2n = 40$ is also reported by Sundermann and von der Bank (1977). **(SD)**

Ecology

Gennaria diphylla is a terrestrial herb with tubers that grows in acid to slightly alkaline soils at elevations of up to 1000 m. It occurs in semi-shaded habitats including pinewoods, forests of bay trees, maquis or garrigue shrubland and may also grow in crevices among rocks (Davies *et al.* 1988; Delforge 1995). It is a characteristic orchid on the island of Madeira where it grows in coastal ravines (Fernandes and Wilcock 1998).

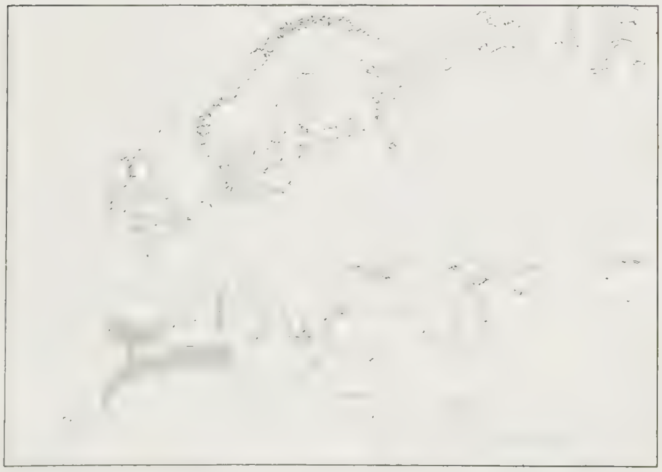

Fig. 76.2. Distribution map of *Gennaria*.

Gennaria diphylla is an early-flowering orchid. In the Canary Islands it can flower in January and elsewhere in the Mediterranean flowers may remain open until April or May. Over much of its range, the species has a localized distribution. It is rare in most of the Mediterranean, especially so in Sardinia, Corsica, and Tunisia. It is frequent only in the Canary Islands (Davies *et al.* 1988; Delforge 1995). **(RN)**

Uses

None recorded. **(PC)**

Cultivation

Compost D. **(CB)**

Taxonomic notes

Lindley (1832, 1835) first placed this species in *Herminium* and then in *Peristylus*, whereas Reichenbach (1851) placed it in *Platanthera.* We are confident that Reichenbach was wrong, but the relationship of *Gennaria* to *Herminium* and *Peristylus* needs further investigation. Its column morphology and the flower structure closely match those of *Peristylus.* **(PC)**

Taxonomic literature

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77. GYMNADENIA

Gymnadenia R.Br. in Aiton, *Hort. Kew.*, ed. **2**, **5**, 191 (1813). Type species: *Gymnadenia conopsea* (L.) R.Br.

Nigritella Rich., *Mém. Mus. Paris*, **4**, 48 (1818). Type species: *Nigritella nigra* (L.) Rchb.f.

Derivation of name

From the Greek *gymnos*, naked, and *aden*, gland, referring to the viscidia that are sometimes free. **(JW)**

Description (Plates 95, 96; Fig. 77.1)

Small slender *herbs. Rootstock* tuberous, tubers flattened, palmate-digitate for at least half their length. *Stem* erect, leafy, especially toward base. *Leaves* basal and cauline, linear to linear-lanceolate, conduplicate, unspotted. *Inflorescence* cylindrical or capitate, densely many-flowered; floral bracts shorter than, equal to, or slightly exceeding ovary. *Flowers* small, resupinate or non-resupinate, fragrant, often of vanilla. *Sepals* and *petals* free and spreading, or lateral sepals spreading and decurved, dorsal sepal connivent with petals to form a hood. *Labellum* shortly three-lobed or entire, spurred, spur

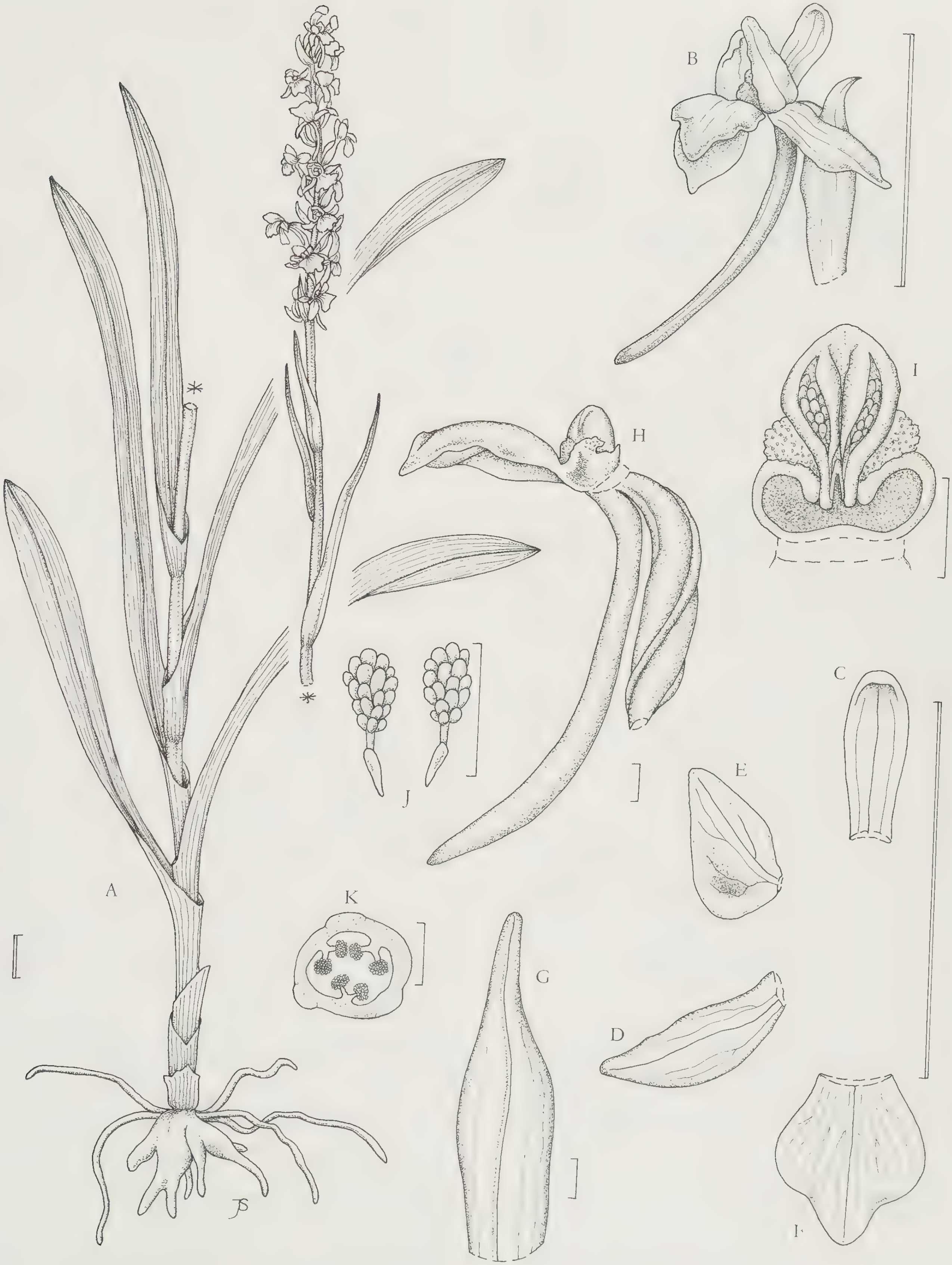

Fig. 77.1. *Gymnadenia conopsea* (L.) R.Br. A. Habit; B. Flower; C. Dorsal sepal; D. Lateral sepal; E. Petal; F. Labellum; G. Bract; H. Labellum and column, side view; I. Column, front view; J. Pollinaria; K. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *McCallum 57* (K) and Kew Spirit Collection no. 34547.

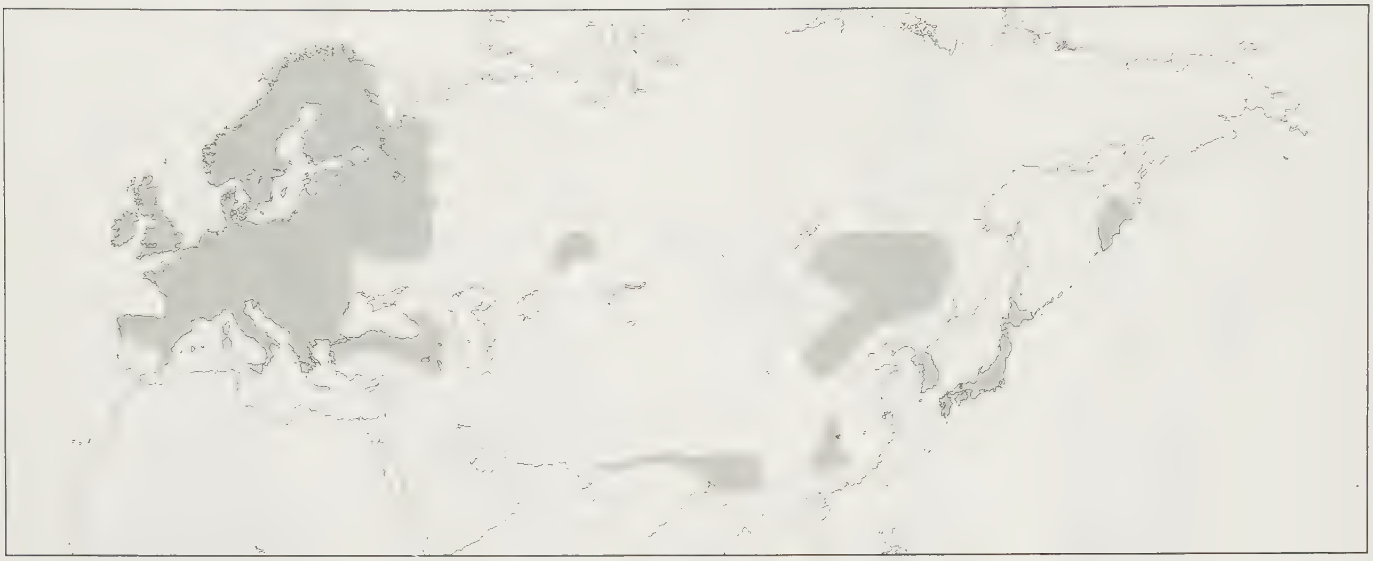

Fig. 77.2. Distribution map of *Gymnadenia.*

short or long, often filiform, nectariferous. *Column* short, with two lateral lobe-like stigmas; rostellum elongate or small, three-lobed, folded between anther loculi; pollinia two, each with a caudicle attached to a free viscidium without a bursicle, or placed in very rudimentary bursicles. *Ovary* narrowly cylindrical, sessile, twisted, or not twisted, glabrous. **(JW)**

Distribution (Fig. 77.2)

About 16 species distributed in Europe, central and eastern Asia including China, Japan, and the Himalayan region. **(JW)**

Palynology

Pollen morphology of *G. odoratissima* is ornate, the muri smooth. The foot layer is verrucose. Baculae are free-standing and irregularly distributed. Sculpturing in *G. albida* Rich. and *G. conopsea* varies between verrucose and hamulate, whereas the sculpturing of *G. nigra* (examined as *Nigritella nigra* (L.) Rchb.f.) resembles that of *G. odoratissima* (Schill and Pfeiffer 1977). **(AP)**

Cytogenetics

Gymnadenia is represented by a diploid cytotype with $2n = 2x = 40$ (Heusser 1938; Teppner and Klein 1985*a*, 1990) and by two polyploid cytotypes with $2n = 4x = 80$ and $2n = 5x = 100$ (Teppner and Klein 1985*b*, 1990, 1998; Wittmann *et al.* 1988; Teppner and Ster 1996). These chromosome numbers reveal that polyploidy is responsible for the evolution of the various species of this genus. The species *G. carpatica*, *G. rhellicani*, *G. gabasiana*, *G. corneliana*, and *G. lithopolitanica* with $2n = 40$ reproduce sexually. On the other hand, *G. nigra*, *G. miniata*, *G. widderi*, *G. stiriaca*, *G. archiducis-joannis*, and *G. dolomitensis* with $2n = 80$ and *G. buschmanniae* with $2n = 100$ are apomictic and produce adventitious (nucellar) embryos (Teppner 1996).

Karyotype morphology is very complex; centromeres can be seen only in the long chromosomes. Thin blocks of telomeric bands are frequent in chromosomes, and large intercalary bands are present in the longest pair (D'Emerico *et al.*, unpublished). **(SD)**

Phytochemistry

Infection of the tubers of *G. nigra* (cited as *Nigritella nigra*) and *G. odoratissima* with a strain of *Rhizoctonia repens* from *Orchis militaris* results in the synthesis of the phytoalexin orchinol (2,4-dimethoxy-7-hydroxy-9,10-dihydrophenanthrene) and *p*-hydroxybenzylalcohol. The compounds were not detected in the bulbs of *G. conopsea* (cited as *Orchis conopsea*) following infection with the same agent. These observations were made as part of a survey of orchinol and *p*-hydroxybenzylalcohol production in a number of species representing genera in subtribe Orchidinae (Nüesch 1963; Gaumann *et al.* 1960).

The leaves of *G. conopsea* contain the flavonols kaempferol and quercetin. These flavonol aglycones were detected in acid-hydrolysed extracts of leaf tissue, indicating that they originate from flavonol *O*-glycosides (C. A. Williams 1979). In an earlier investigation, the flavonol *O*-glycosides, kaempferol 3-*O*-β-D-glucoside (astragalin), kaempferol 3,7-di-*O*,*O*-β-D-glucoside (paenoside), quercetin 3-*O*-β-D-glucoside (isoquercitrin), and quercetin 3,7-di-*O*,*O*-β-D-glucoside were found in the same species (Schönsiegel and Egger 1969). Uphoff (1979) investigated the anthocyanin content of the flowers of several *Gymnadenia* species. *Gymnadenia conopsea*, *G. miniata* (cited as *N. miniata*), and *G. odoratissima* contain cyanidin 3,5-diglucoside (cyanin) and the pigments orchicyanin I and II in the ratio 10:50:40, respectively. In contrast, *G. nigra* flowers contain only cyanidin 3-glucoside (chrysanthemin). Strack *et al.* (1989) found chrysanthemin, cyanin, seranin, ophrysanin, serapianin, and orchicyanins I and II in *G. conopsea* and *G. odoratissima.* Orchicyanins I and II, ophrysanin, and serapianin were identified as cyanidin glucosides acylated with oxalic acid (Strack *et al.* 1986, 1989).

The chemical composition of the scent of *G. conopsea* and *G. nigra* flowers was obtained by gas chromatography coupled with mass spectroscopy (Kaiser 1993). The scent composition of *G. conopsea* flowers varies among different plants, although the principal components are always benzyl acetate and benzyl benzoate. The principal components of the scent of *G. nigra* are benzyl alcohol and phenylethyl alcohol. However, a series of compounds commonly found in extracts of vanilla and cocoa are also present as minor components, including vanillin, vanillyl ethyl ether, phenylacetaldehyde, isovaleraldehyde, and benzyl isovalerate. These contribute to the characteristic 'vanilla' fragrance of this species. **(NV, RG)**

Ecology

Gymnadenia grows on a variety of soil types but is most common on calcareous soils such as limestone and chalk with high calcium levels (Summerhayes 1951). A calcium measurement of 780 mg/ 100 g soil was recorded for soils supporting *G. 'verna'* by O. Möller in 1985 (Arditti 1992). Some *Gymnadenia* species, such as *G. conopsea* subsp. *borealis* (Druce) F. Rose in Scotland, occur on more acidic soils (Davies *et al.* 1988). Similarly, *Gymnadenia nigra* can grow in soils with a low calcium content such as the riverbank habitats described from Sweden by Bjorkback and Lundqvist (1996), but generally it occurs on calcareous soils (Rune 1993). Soil moisture preferences vary considerably between members of the genus and encompass both comparatively dry and very wet habitats. For example, in Britain *G. conopsea* subsp. *conopsea* typically grows in dry grasslands such as the chalk downlands of southern England (Summerhayes 1951; Lang 1989), whereas *G. conopsea* subsp. *densiflora* is always found in wet marshes and bogs, as in the East Anglian fens (Sanford 1991). Rasmussen (1995) noted for *Gymnadenia nigra* that although the plants grow in damp conditions, the shallow soils and drying winds of the habitats they inhabit may create conditions of comparative drought.

Gymnadenia normally grows in full sun in open habitats such as grassland, mountain pastures, base-rich mires and fen meadows (Delforge 1995; Eysink and De Bruijn 1997) and sometimes roadside verges or wet ditches (Allan *et al.* 1993). However, it can withstand some shade since in some parts of its range it is found growing in heathland, scrubland, and open woodland (Summerhayes 1951), and in Russia it has been reported from pine forests (Davies *et al.* 1988). In the Mediterranean *G. conopsea* occurs primarily in mountain areas where it grows at elevations of up to 2500 m. *Gymnadenia nigra* usually grows in grassland and alpine meadows but may also occur in open wooded pastures and on woodland edges (Davies *et al.* 1988; Delforge 1995). It grows at high elevations of 1000–2800 m, in the mountains of central Europe, such as the Alps, Carpathians, Appenines, and Pyrenees, but in Scandinavia it normally grows at lower elevations in subalpine or low alpine regions (Engelskjon and Skifte 1984; Davies *et al.* 1988). In the Swedish province of Jämtland, *G. nigra* is largely confined to cultivated farmsteads but has also been discovered growing in the same region at sites on the banks of streams (Bjorkback *et al.* 1986; Bjorkback and Lundqvist 1996).

Depending on the habitat in which they occur, *Gymnadenia* species can co-occur with a range of other orchids. On the chalk downland of southern England for example, *G. conopsea* can be found in short grassland with *Ophrys apifera* Huds., *Neotinea ustulata* (L.) R. M. Bateman, Pridgeon & M. W. Chase, and *Herminium monorchis* (L.) R.Br., and with *Dactylorhiza fuchsii*, *Anacamptis pyramidalis* or *Listera ovata* (L.) R.Br. among taller grasses. In the limestone areas of northern England it also grows with *Platanthera chlorantha* (Custer) Rchb., *Dactylorhiza viridis*, and *Orchis mascula* (L.) L., while in upland pastures at up to 700 m it may be accompanied by *P. bifolia* (L.) Rich., *D. purpurella*, and *Pseudorchis albida* (L.) Á. Löve & D. Löve. In the more acidic soils of British heathland habitats it is sometimes found growing among *Calluna* and *Ulex* species with *D. maculata* subsp. *ericetorum*, whereas in wetland areas where *Gymnadenia* grows among sedges and coarse grasses (e.g. *Carex* and *Molinia* species) typical co-occurring orchids include *D. praetermissa* and *Epipactis palustris* (L.) Crantz (Summerhayes 1951; Lang 1989).

Gymnadenia flowers between May and August throughout its range (Delforge 1995), the exact period of flowering depending on the latitude and locality of individual populations. In Britain, for example, most flower in June (Lang 1989), although plants growing in drier sites usually flower before those in damper soils (Summerhayes 1951). Leaves of *Gymnadenia* develop in the spring prior to flowering and are retained until the autumn ('summer-green' orchids), the plants perennating over the winter by means of tubers (Möller 1987, cited in Rasmussen 1995). The number of plants emerging above ground and flowering in populations of *G. conopsea* is reportedly highly variable between years, an observation which has variously been explained as due to differences in establishment success of seedlings and young plants between seasons (Summerhayes 1951), annual changes in rainfall patterns (Allan *et al.* 1993), a short lifespan, and frequent monocarpy (Salisbury 1942).

Fruit-set level is generally high within the genus (Lang 1989). Summerhayes (1951) reported that between 50% and 90% of the flowers of *G. conopsea* produce seed capsules, and Neiland (1994) has recorded an average of 63.3% of flowers setting fruit in study populations in Britain. Salisbury (1942) has explained the failure of the uppermost flowers on some inflorescences to set fruit as the result of nutritional constraints. Relatively high fruit-set is to be expected in *Gymnadenia* since many members of the genus are nectariferous (Neiland and Wilcock 1998), but this is also due to apomixis in some species (Delforge 1995). An average of 2044 ± 515 seeds are estimated to be produced by each capsule of *G. conopsea* (Salisbury 1942). Seed germination is believed to take place in the spring after dispersal, following a period of chilling in the winter that is thought to break seed dormancy (Fuchs and Ziegenspeck 1927, cited in Rasmussen 1995). In culture, seeds of *G. nigra* take 2–3 months to germinate *in vitro* (Veyret 1969; Haas 1977, cited in Rasmussen 1995), whereas some immature seeds excised about one month after pollination could be rapidly germinated with just two weeks of incubation (Malmgren 1989, cited in Rasmussen 1995). In the field, the first aerial stem forms about two years after germination, the seedlings having already developed roots in the previous autumn. The first tuber is formed in the summer. Adult plants perennate by means of tubers during the winter, gaining nutrition at this time from mycotrophic roots, which are normally found in the upper layers of the soil in *G. conopsea* (Rasmussen 1995). Beau (1913) also found fungi in the tapering extensions of the tuber, and a number of different fungi have been identified including *Rhizoctonia solani* (Anderson 1990*a*) and *Tulasnella* spp., although not all are compatible with *Gymnadenia* seedlings. Downie (1959) failed to germinate *G. conopsea* with a fungus isolated from adult plants, although Anderson (1990*b*) was successful with *Tulasnella calospora* and another *Tulasnella* species (Rasmussen 1995).

The frequency of occurrence and rarity of *Gymnadenia* species varies among the species and across their geographic range. The widespread *G. conopsea*, for example, is quite localized in its occurrence in some parts of its range, as in the British Isles, where it is not considered to be a common orchid even though it can be abundant in some places (Summerhayes 1951). In Scotland, *G. conopsea* subsp. *borealis* is the most common of the three subspecies and has been recorded from every Scottish vice-county (Allan *et al.* 1993). The distribution of the other two subspecies (ssp. *densiflora* and ssp. *conopsea*) is severely restricted by habitat and soil limitations such that they are extremely rare in Scotland but more frequent in southern England. *Gymnadenia nigra* can occur in large numbers in the Alps, but it has become a rare and endangered species in Scandinavia due to a loss of suitable habitats such as hay meadows (Bjorkback and Lundqvist 1996; Rune 1993). In the absence of grazing or mowing *G. nigra* becomes shaded and out-competed by more vigorous plants (Bjorkback *et al.* 1986). Habitat changes also threaten other members of the genus. A steady decline in the size of one *G. conopsea* population in Scotland was attributed to overgrowth of heather at the site (Dickson and Parkes 1994), and drainage of fenland is identified as the major threat to the remaining populations of *G. conopsea* subsp. *densiflora* in Suffolk, England (Sanford 1991).

Remedial measures, such as removing shrubs by hand, have been suggested as means by which *Gymnadenia* populations can be protected (e.g. Dickson and Parkes 1994), and in Sweden a conservation programme has been underway for several years to maintain *G. nigra* populations using different management regimes aimed at keeping the habitats open and thereby preventing shading out of the orchid by more vigorous plants (Bjorkback *et al.* 1986). **(RN)**

Pollination

Species of the genus *Gymnadenia* (excluding the former *Nigritella* spp.) are all considered nectariferous and pollinated by butterflies and hawk-moths. Flowers of *G. conopsea* are highly variable in floral morphology, colour, and scent and are pollinated by both butterflies and hawk-moths, demonstrating that differences between moth flowers and butterfly flowers may be continuous (van der Pijl and Dodson 1966). *Gymnadenia odoratissima*, on the other hand, seems to be pollinated predominantly by hawk-moths (van der Cingel 1995). Members of the former genus *Nigritella* are only partly dependent on insects for reproduction. Diploid taxa are pollinated by Lepidoptera, e.g. *Zygaena*, which visit flowers in large numbers. Polyploid taxa on the other hand, such as the Scandinavian *G. nigra*, are apomicts (Timpe and Mrkvicka 1991). **(AW, SC, AD)**

Uses

None recorded. **(JW)**

Cultivation

Throughout their range plants often grow at higher elevations on calcareous soils. In cultivation they should do well in compost C with added lime. **(CB)**

Taxonomic notes

Recent molecular systematic studies by Pridgeon *et al.* (1997) and Bateman *et al.* (1997) supported the conclusions of Sundermann (1980), who treated *Nigritella* within *Gymnadenia*. Despite superficial differences in flower form and resupination, *Nigritella* shares several morphological characters with *Gymnadenia*: palmate-digitate tubers; two lateral, lobe-like stigmas; and two pollinia each with a caudicle attached to free, naked or partially naked viscidia. **(JW)**

Taxonomic literature

Bateman, R. M., Pridgeon, A. M., and Chase, M. W. (1997). Phylogenetics of subtribe Orchidinae (Orchidoideae, Orchidaceae) based on nuclear ITS sequences. 2. Infrageneric relationships and reclassification to achieve monophyly of *Orchis sensu stricto*. *Lindleyana*, **12**, 113–41.

Breiner, E. and Breiner, R. (1990). Contribution à la taxonomie du genre *Nigritella*. *Orchidophilie*, **11**, 15–31.

Sundermann, H. (1980). *Europäische und Mediterrane Orchideen*, ed. 3. Schmersow, Hildesheim.

Teppner, H. and Klein, E. (1990). *Nigritella rhellicana spec. nova.* und *N. nigra s.st. Phyton* (*Austria*), **31**, 5–26.

78. HABENARIA

Habenaria Willd., *Sp. Pl.* ed. 4, 44 (1805). Type species: *H. macroceratitis* Willd. (lectotype selected by Kränzl., *Bot. Jahrb. Syst.*, **16**, 58, 1892).

Habenorkis Thouars, *Nouv. Bull. Soc. Philom.*, n. 19, 317 (1809).

Centrochilus Schauer, *Nov. Act. Nat. Curios.*, **19**, *Suppl.* **1**, 435, t. 13C (1843). Type species: *C. gracilis* Schauer

Dissorhynchium Schauer, *Nov. Act. Nat. Curios.*, **19**, *Suppl.* **1**, 434, t. 13A (1843). Type species: *D. muricatum* Schauer

Montolivaea Rchb.f., *Otia Bot. Hamb.*, 107 (1881). Type species: *Montolivaea elegans* (Lindl.) Rchb.f.

Podandria Rolfe, *Fl. Trop. Afr.*, **7**, 205 (1898), *non* Baill. (1890), *nom. illegit.* Type species: *P. macrandra* (Lindl.) Rolfe

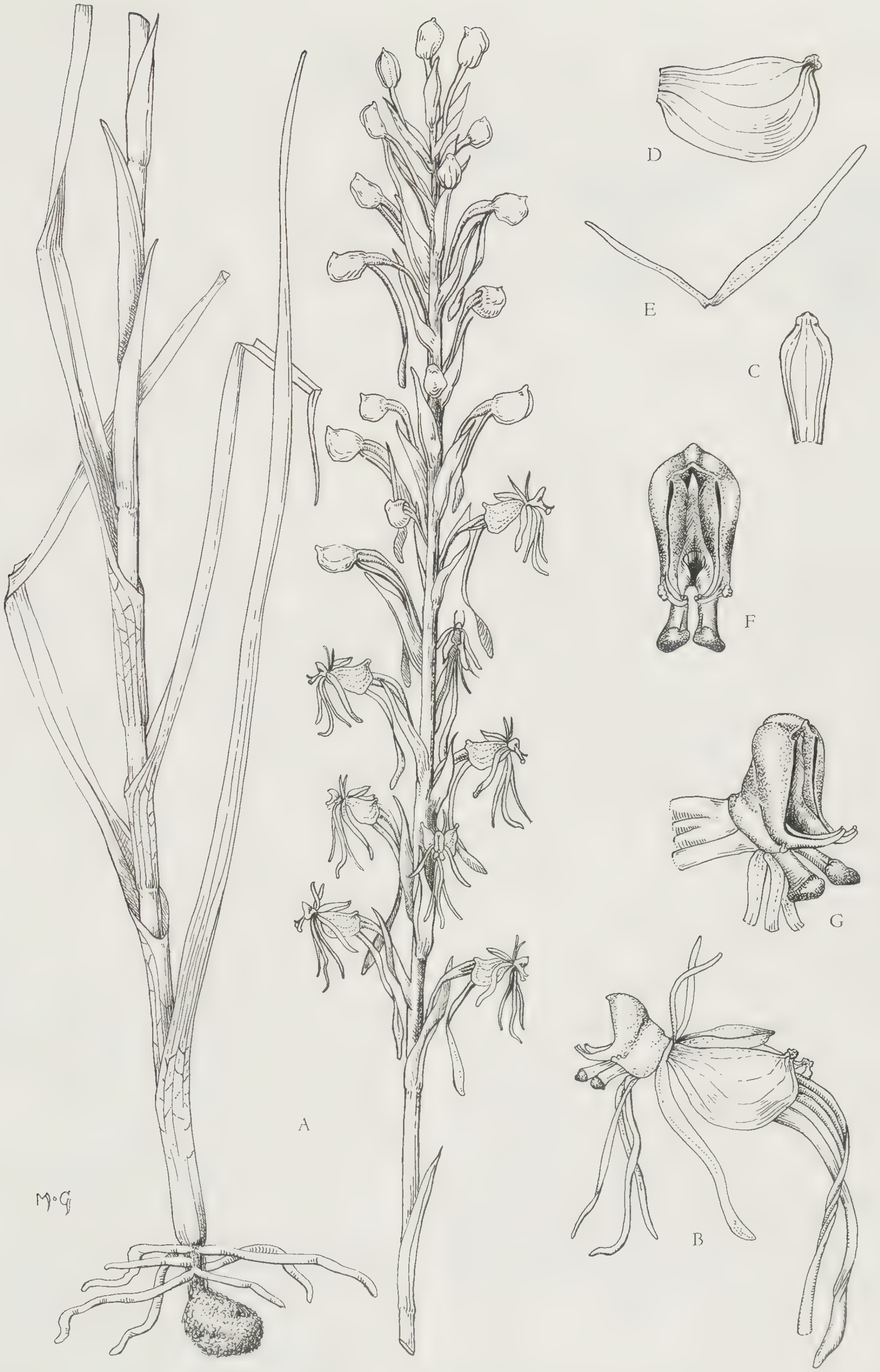

Fig. 78.1. *Habenaria compta* Summerh. A. Habit, ×1; B. Flower, ×3; C. Dorsal sepal, ×4; D. Lateral sepal, ×4; E. Petal, ×4; F. Column, front view, ×4; G. Column, oblique view, ×4. Drawn by Mary Grierson from *Richards 5867*.

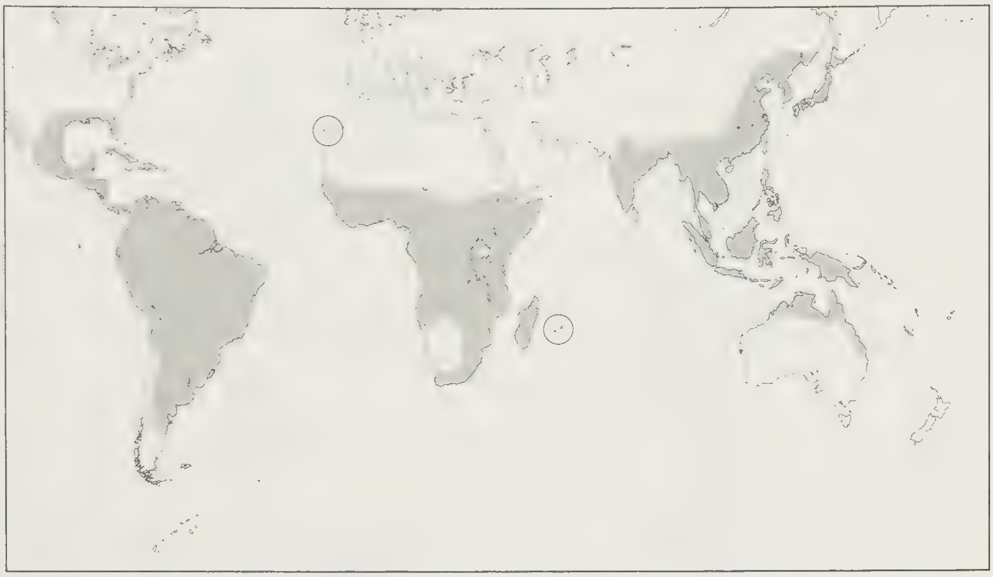

Fig. 78.2. Distribution map of *Habenaria.*

Kryptostoma (Summerh.) Geerinck, *Bull. Jard. Bot. Nat. Belgique*, **52**, 149 (1982). Type species: *Habenaria tentaculigera* Rchb.f.

Ala Szlachetko, *Fragm. Fl. Geobot. Suppl.*, **3**, 113 (1995), *nom. inval.* Type species: *H. decorata* Hochst. ex A. Rich.

Podandriella Szlachetko & Olszewski, *Fl. Cameroun Orchidées*, **1**, 192 (1998), **synon. nov.** Type species: *Habenaria macrandra* Lindl.

Pseudoperistylus (P. F. Hunt) Szlachetko & Olszewski, *Fl. Cameroun Orchidées*, **1**, 192 (1998), **synon. nov.** Type species: *Habenaria petitiana* A. Rich.

Derivation of name

From the Latin *habena*, reins, referring to the long, strap-like divisions of the petals and lip. **(PC)**

Description (Plates 97, 98; Fig. 78.1)

Terrestrial, rarely epiphytic, *herbs* with hairy tubers or long fleshy roots. *Stem* unbranched. *Leaves* several–many, lanceolate, ovate oblong or elliptic, sheathing at the base, arranged along stem or clustered at the base or in the middle, or with 1–2 basal leaves appressed to the ground and the cauline leaves sheath-like. *Inflorescence* terminal, one- to many-flowered. *Flowers* usually resupinate, green and/or white, rarely with a yellow, pink, or red labellum. *Sepals* usually free, the dorsal sepal often forming a hood with the petals; lateral sepals spreading or reflexed. *Petals* entire, two-lobed or bifid. *Labellum* entire or three-lobed, spurred at base; the side lobes sometimes divided; the spur long or short, slender or saccate, often inflated at apex. *Column* long or short; anther erect or reclinate, the loculi either adjacent or separated by a U-shaped connective; anther canals long or short, almost always adnate to side lobes of rostellum; lateral appendages two, sometimes two-lobed; pollinaria two, each with a sectile pollinium, long or short caudicle, and a small, naked viscidium; stigmatic processes two, long or short, usually free but sometimes joined in lower part to rostellum. **(PC)**

Distribution (Fig. 78.2)

A genus of about 600 species, in tropical and subtropical regions of Old and New World. **(PC)**

Infrageneric treatment (PC)

The following sectional treatment, which certainly needs radical reassessment, is based on a modified version of that of Kränzlin:

Habenaria section **Anomalae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 56, 206 (1893). Type species: *H. anomala* Lindl.

Habenaria section **Ate** Lindl., *Gen. Spec. Orch. Pl.*, 326 (1840). Type species not designated.

Habenaria section **Ceratopetalae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 55, 64 (1893). Type species: *H. cornuta* Lindl., lectotype selected by Summerhayes, *Fl. Trop. E. Afr. Orch.*, **1**, 39 (1968).

Habenaria section **Chlorinae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 56, 156 (1893). Type species: *H. chlorina* Par. & Rchb.f., lectotype selected by Summerhayes, *Fl. Trop. E. Afr. Orch.*, **1**, 39 (1968).

Habenaria section **Clypeatae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 56, 139 (1893). Type species not designated.

Habenaria section **Commelynifoliae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 56, 136 (1893). Type species: *H. commelynifolia* Lindl., lectotype selected by Summerhayes, *Fl. Trop. E. Afr. Orch.*, **1**, 39 (1968).

Habenaria section **Cruciatae** Kränzl., *Orch. Gen. Sp.*, **1**, 425 (1898). Type species not designated.

Habenaria section **Cultratae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 55,88 (1893). Type species: *H. cultrata* A. Rich., lectotype selected by Summerhayes, *Fl. Trop. E. Afr. Orch.*, **1**, 39 (1968).

Habenaria section **Diphyllae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 56, 147 (1893). Type species: *H. diphylla* Dalz., lectotype selected by Summerhayes, *Fl. Trop. E. Afr. Orch.*, **1**, 39 (1968). Syn.: *H.* sect. *Geophyllum* Schltr., *Bot. Jahrb. Syst.*, **53**, 501 (1915). Type species not designated.

Habenaria section **Dolichostachyae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 55, 103 (1893). Type species not designated.

Habenaria section **Kryptostoma** Summerh., *Kew Bull.*, **14**, 135 (1960). Type species: *H. tentaculigera* Rchb.f.

Habenaria section **Macroceratitae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 55 (1893). Type species not designated.

Habenaria section **Macrurae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 55, 91 (1893). Type species: *H. perbella* Rchb.f., lectotype selected by Summerhayes, *Fl. Trop. E. Afr. Orch.*, **1**, 39 (1968).

Habenaria section **Maculosae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 56, 128 (1893). Type species not designated.

Habenaria section **Microdactylae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 55, 100 (1893). Type species not designated.

Habenaria section **Medusaeformes** Kräenzl., *Bot. Jahrb. Syst.*, **16**, 55, 102 (1893). Type species not designated.

Habenaria section **Micranthae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 55. 112 (1893). Type species not designated.

Habenaria section **Microstylinae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 56, 187 (1893). Type species not designated.

Habenaria section **Mirandae** Summerh., *Kew Bull.*, **16**, 301 (1962). Type species: *H. rautenaniana* Kränzl.

Habenaria section **Multipartitae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 56, 156 (1893). Type species: *H. multipartita* Blume, lectotype selected by Summerhayes, *Fl. Trop. E. Afr. Orch.*, **1**, 39 (1968). Syn.: *H.* sect. *Taenianthera* Schltr., *Bot. Jahrb. Syst.*, **53**, 499 (1915). Type species not designated; *Ala* Szlachetko, *Fragm. Fl. Geobot. Suppl.*, **3**, 113 (1995), *nom. inval.* Type species: *H. decorata* Hochst. ex A. Rich.

Habenaria section **Odontopetalae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 56, 217 (1893). Type species not designated.

Habenaria section **Pentaceras** (Thou.) Schltr., *Bot. Jahrb. Syst.*, **53**, 496 (1915). Type species: *H. arachnoides* Thou., lectotype selected by Summerhayes, *Fl. Trop. E. Afr. Orch.*, **1**, 39 (1968).

Habenaria section **Pentadactylae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 55, 114 (1893). Type species not designated.

Habenaria section **Peristyloideae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 56, 176 (1893). Type species not designated.

Habenaria section **Plantaginea** Kränzl., *Bot. Jahrb. Syst.*, **16**, 56, 194 (1893). Type species not designated.

Habenaria section **Plectoglossa** Hook.f.., *Fl. Brit. India*, **6**, 132, 164 (1890). Type species not designated.

Habenaria section **Podandria** (Rolfe) P. F. Hunt, *Kew Bull.*, **22**, 489 (1968). Type species: *H. macrandra* Lindl.

Habenaria section **Pratenses** Kränzl., *Bot. Jahrb. Syst.*, **16**, 56, 125 (1893). Type species not designated.

Habenaria section **Productae** Summerh., *Kew Bull.*, **20**, 167 (1966). Type species: *H. singularis* Summerh.

Habenaria section **Pseudoperistylus** P. F. Hunt, *Kew Bull.*, **22**, 489 (1968). Type species: *H. petitianana* (A. Rich.) Th. Dur. & Schinz.

Habenaria section **Quadratae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 56, 182 (1893). Type species not designated.

Habenaria section **Replicatae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 74, 85 (1893). Type species: *H. kilimanjari* Rchb.f., lectotype selected by Summerhayes, *Fl. Trop. E. Afr. Orch.*, **1**, 39 (1968).

Habenaria section **Salaccenses** Kränzl., *Bot. Jahrb. Syst.*, **16**, 55, 83 (1893). Type species not designated.

Habenaria section **Seticaudae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 55, 250 (1893). Type species not designated.

Habenaria section **Spathaceae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 55, 94 (1893). Type species not designated.

Habenaria section **Trachypetalae** Summerh., *Bot. Mus. Leafl. Harv. Univ.*, **10**, 264 (1942). Type species: *H. trachypetala* Kränzl.

Habenaria section **Tridactylae** Kränzl., *Bot. Jahrb. Syst.*, **16**, 56, 141 (1893). Type species not designated.

Palynology

Schill and Pfeiffer (1977) examined the pollen of five species of *Habenaria*. Sculpturing *of H. macranda*, *H. medusa* (cited as *H. medusae*), and *H. rhodocheila* is ornate. Muri are ± smooth. Baculae are irregularly distributed. Sculpturing in *H. arenaria* and *H. tridactylis* [*sic*] is hamulate. It is unclear whether the latter species is correctly *H. tridactyla* A. Rich. or *H. tridactylites* Lindl. **(AP)**

Cytogenetics

The genus *Habenaria*, according to the reports in the literature, presents a great variety of chromosome numbers from $2n = 28$ to 168. The predominance of number $2n = 42$ shows that this genus is actually based on $x = 21$. Moreover, the presence of two species with $2n = 28$ indicates that the ancestral basic number for the genus is $x = 7$, and all the north-west Himalayan species are hexaploid (Mehra and Bawa 1970). Cytological studies in *Habenaria* revealed numerous species with diploid chromosome number $2n = 2x = 42$ and interesting variation in the numbers for the species (see Table C.2). Cases of dysploidy with $2n = 28$, 30, 38, 40, 44, 62, 64, 122 and 134 are also known (Tanaka and Kamemoto 1980). **(SD)**

Phytochemistry

The bioassay-guided fractionation and isolation of bis-*p*-hydroxybenzyl-2*S*-isobutylmalate (habenariol; Fig. 78.3) from a dichloromethane extract of the whole plant of the semi-aquatic orchid, *Habenaria repens*, has been reported recently (Wilson *et al.* 1999). This compound deters feeding by the common freshwater crayfish, *Procambarus clarkii*, and is an example of chemical defence against an aquatic herbivore. Habenariol is identical to the aglycone of the

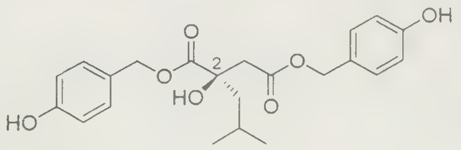

Fig. 78.3. Habenariol.

phenolic glucoside militarine from *Orchis militaris*, with the exception of the configuration at C-2 (Fig. 81.4). In habenariol, the (*S*)-configuration was assigned to C-2 on the basis of optical rotation data and comparison with data for synthetic 2-alkylmalic acids (Wilson *et al.* 1999). Militarine adopts the (*R*)-configuration at C-2 (Aasen *et al.* 1975). **(NV, RG)**

Ecology

Species of the widespread genus, *Habenaria*, are usually terrestrial orchids that perennate by means of underground tubers. More rarely they are epiphytic herbs, such as *H. procera* Lindl., which often grows on oil palm trees (*Elaeis guineënsis* A. Cheval.) in western Africa and is typically found among ferns and mosses in lowland rain forest in eastern Africa (Summerhayes 1968). Throughout the range of the genus, *Habenaria* species frequently grow in damp or wet habitats including marshes, bogs, water meadows, seasonally flooded grasslands ('dambos' and 'vleis' in Africa), seepage slopes and wet flushes on hillsides, riverbank habitats, swamp forest, and tropical wet evergreen forest (Holttum 1964; Ohwi 1965; Summerhayes 1968; Miller 1978; Polunin and Stainton 1984; la Croix and Cribb 1995). Some species even grow in standing or slowly running water. Other members of the genus inhabit drier areas such as grassland and dry deciduous woodland (la Croix and Cribb 1995). A few African species are reported to occur on old termite mounds (e.g. *H. armatissima* Rchb.f.), and other *Habenaria* orchids frequently grow in stoney soil or shallow soil among rocks, which may be either wet or dry. The underlying substrate from areas in which *Habenaria* species grow includes limestone, granite, quartzite, and laterite (Holttum 1964; la Croix and Cribb 1995). Soil types range from peaty to sandy (Summerhayes 1968; la Croix and Cribb 1995).

Habenaria species growing in open or exposed habitats, such as montane grasslands, receive high light-levels, but others are shade-tolerant plants that occur in deciduous or evergreen woodlands throughout the range of the genus. In Africa *Habenaria* grows in a variety of vegetation types including *Brachystegia* (Fabaceae), *Uapaca* (Euphorbiaceae), and *Cryptosepalum* (Fabaceae) woodlands, mopani bush, *Syzgium* (Myrtaceae) thickets, Miombo woodland, and *Eucalyptus* (Myrtaceae) and pine plantations (la Croix and Cribb 1995). In Papua New Guinea, *Habenaria* species are common in the Morobe lowland rainforests growing in the deep litter of the forest floor (Millar 1978), and in the United States *H. quinqueseta* (Michx.) Sw. occurs in pine and other woods in the southern states of America (Rickett 1966).

Habenaria species grow at a wide range of elevations from lowlands to high montane areas. For example, in South Africa *H. arenaria* Lindl. occurs only in coastal bush on stabilized sand-dunes (Schelpe 1966), and in Japan species such as *H. sagittifera* Rchb.f. are typically found in bogs and wet grasslands at low elevations (Ohwi 1965). Other species are mountain plants. *Habenaria pectinata* D. Don occurs in the Himalayas up to 3000 m (Hooker 1894; Polunin and Stainton 1984) and in Uganda, Kenya, and Ethiopia at 2200–3300 m in upland moorland. *Habenaria bracteosa* Hochst. ex A. Rich., a mountain-forest species from eastern Africa, grows above the forest zone at 2200–3600 m (Summerhayes 1968). Some species grow across a wide elevational range, for example the widespread tropical African orchids *H. welwitschii* Rchb.f. and *H. arianae* D. Geerinck, which grow in grasslands at elevations of 0–2000 m and 600–2300 m, respectively.

Flowering of *Habenaria* usually takes place from July to October or October to January in different parts of Asia (Ohwi 1965; Dassanyake 1981; Polunin and Stainton 1984), from August to January in the United States (Rickett 1966), and between October and April (to June) in tropical Africa (la Croix and Cribb 1995). Fruit-set data have been collected in tropical Africa (la Croix and Cribb 1995), and levels of reproductive success could be expected to be high given that members of the genus are nectariferous (Neiland and Wilcock 1998). New tubers probably begin to form following flowering and are the means by which the plants survive the dry season in some regions. Tubers may also allow vegetative spread. For example, la Croix and Cribb (1995) noted that *H. nyikensis* G. Williamson, a species endemic to Malawi, rarely flowers but does form large colonies in open montane grassland and *Brachystegia* woodland habitats. Mycorrhizal associations have been investigated for some *Habenaria* species, such as *H. rariflora* from southern India, the root systems of which were heavily infected with mycorrhiza (Raja *et al.* 1996). At least one species, *H. saprophytica* J. Bosser & P. J. Cribb, is reported to be achlorophyllous (Bosser and Cribb 1996).

Habenaria includes both rare and common species. Some are endemics with restricted distributions, for example *H. pubipetala* Summerh. which is confined to six localities in Malawi (la Croix 1994). Others have become scarce through over-collection, such as *H. carnea* N. E. Br. in Malaysia (Holttum 1964). In China, *H. delavayi* Finet and *H. dentata* Schltr. are collected for use in herbal medicine (Chen and Tang 1982). Cribb noted that *H. taeniodema* Summerh. from the highlands of Ethiopia is possibly on the verge of extinction because of threats to its scrubland habitat and collection of the plant itself (IUCN Orchid Specialist Group 1996). Pradhan (IUCN Orchid Specialist Group 1996) listed five *Habenaria* species as among the most threatened orchids in India, either because of their localized distribution (e.g. *H. pseudophrys* King & Pantl.) or because thay have not been recorded for a long time (e.g. *H. pachycaulon* Hook.f.). Cadet (1989) suggested that three endangered *Habenaria* species should be protected on the island of Réunion in the Mascarenes. **(RN)**

Uses

A few species are cultivated, notably the Asiatic *H. rhodocheila*, which has a red or yellow lip.

Lawler (1984) listed several uses for *Habenaria* species. Some species have been used as charms. *Habenaria dives* Rchb.f., *H. dregeana* Lindl., and *H. epipactidea* Rchb.f. were used as charms in South Africa, the first as a death charm; tubers are mixed with food and the victim then expected to waste away (Rayner 1977). The tubers of *H. walleri* Rchb.f. in Malawi have been used as food, prepared in the form of a jelly, which is boiled with salted water and served with peanuts as a side dish (Williamson 1955). *Habenaria acuminata* Thw. ex Trimen. and *H. commelinifolia* Lindl. are both used as food in India, the latter boiled to make a gruel (Duggal 1972; Usher 1974). *Habenaria* tubers are used as famine food and fed to pigs in New Guinea (Massal and Barrau 1955; Treide 1967; Powell 1976). The tubers of *H. multipartita* Bl. ex Kränzl. are eaten in Java (Bakhuisen van der Brink 1937), as are those of *H. rumphii* Lindl. in Ambon (Rumphius 1741–1750; Smith 1927).

A decoction of the boiled tubers is widely used medicinally: an infusion of boiled tubers of *H. cirrhata* Rchb.f. for curing indigestion in Kenya (Kokwaro 1976); *H. macrandra* Lindl. as a purgative, and *H. walleri* Rchb.f. for stomach diseases in East Africa (Kokwaro 1976); *H. ciliolaris* Kränzl. for internal injuries in Sichuan, China (Cheo 1947, Hu 1971 *a*, *b*); *H. sp.* for infected wounds in Indo-China (Dournes 1955); *H. miersiana* Champ. ex Benth. for dressed wounds and swellings by aboriginal people in Taiwan; and for colic in Sichuan (Cheo 1947, Liu 1952; Hu 1971 *a*, *b*). An infusion of the tubers of *Habenaria* species has been used in South Africa to promote fertility (Rayner 1977). Salep, used as food and an aphrodisiac or restorative in India and Myanmar (Burma), is produced from the tubers of *H. commelinifolia* and other species (Chopra *et al.* 1956; Kirtikar and Basu 1918; Nair 1963). **(PC)**

Cultivation

Terrestrials, bog and semi-aquatic plants, lithophytes or epiphytes. Many sturdy and showy species of easy cultivation. Composts A, B, C, or D. **(CB)**

Taxonomic notes

Kränzlin (1893, 1987–1904) monographed the genus *Habenaria*, recognizing 427 species in 32 sections, and current infrageneric classification is based upon his work. The major characters that he used to divide the genus into sections were degree of dissection of the lip as well as features of the petals and column. Inevitably some of the sections are artificial and contain unrelated taxa. Schlechter (1915) renamed some of Kränzlin's sections. Summerhayes (1942, 1960, 1962, 1966) and Hunt (1968) produced some refinements to Kränzlin's system, recognizing additional sections mainly based upon African species. Some of Kränzlin's sections, such as *Bonatea* and *Platycoryne*, have regained generic rank in treatments by later authors. Recently, Szlachetko and Olszewski (1998) raised further sections to generic rank, but this has not yet been widely followed. A conservative view has been taken here because of the piecemeal nature of much of the work to date. Molecular analyses may well lead to the recognition of some of the sections at a higher rank. The limited molecular data gathered and analysed to date indicate that *Habenaria*, as currently understood, is polyphyletic. Alternatively, some genera such as *Bonatea*, *Centrostigma*, *Platycoryne*, and *Roeperocharis* could be included within a more broadly defined *Habenaria*. **(PC)**

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79. HEMIPILIA

Hemipilia Lindl., *Gen. Sp. Orch. Pl.*, 296 (1835). Type: *H. cordifolia* Lindl.

Derivation of name

From the Greek *hemi*, semi, and *pilos*, felt, in allusion to the lip of the type, which is covered irregularly with felt-like hairs. **(PC)**

Description (Plate 99; Fig. 79.1)

Small to medium-sized terrestrial *herbs* growing from ovoid or subspherical tubers. *Leaf* solitary, fleshy, basal, appressed to substrate, elliptic-ovate to heart-shaped, green, grey-green or variously mottled or flecked with dark purple on upper surface. *Inflorescence* erect, laxly to subdensely few- to several-flowered; bracts lanceolate, green, glabrous. *Flowers* usually purple or purple-marked. *Dorsal sepal* free, concave, sometimes adnate to petals to form a hood over the column, glabrous. *Lateral sepals* free, spreading. *Petals* smaller than the dorsal sepal, free or adnate to the dorsal sepal. *Labellum* entire or three-lobed, deflexed to porrect, ecallose, spurred at the base; spur elongate, straight or occasionally incurved. *Column* erect; anther subhorizontal, loculi divergent toward base; pollinia two, sectile, clavate; viscidia two, concealed by the incurved apices of the stigma lobes; stigma bilobed; rostellum three-lobed, the mid-lobe porrect, large, the side lobes fleshy, incurved. *Ovary* more or less sessile. **(PC)**

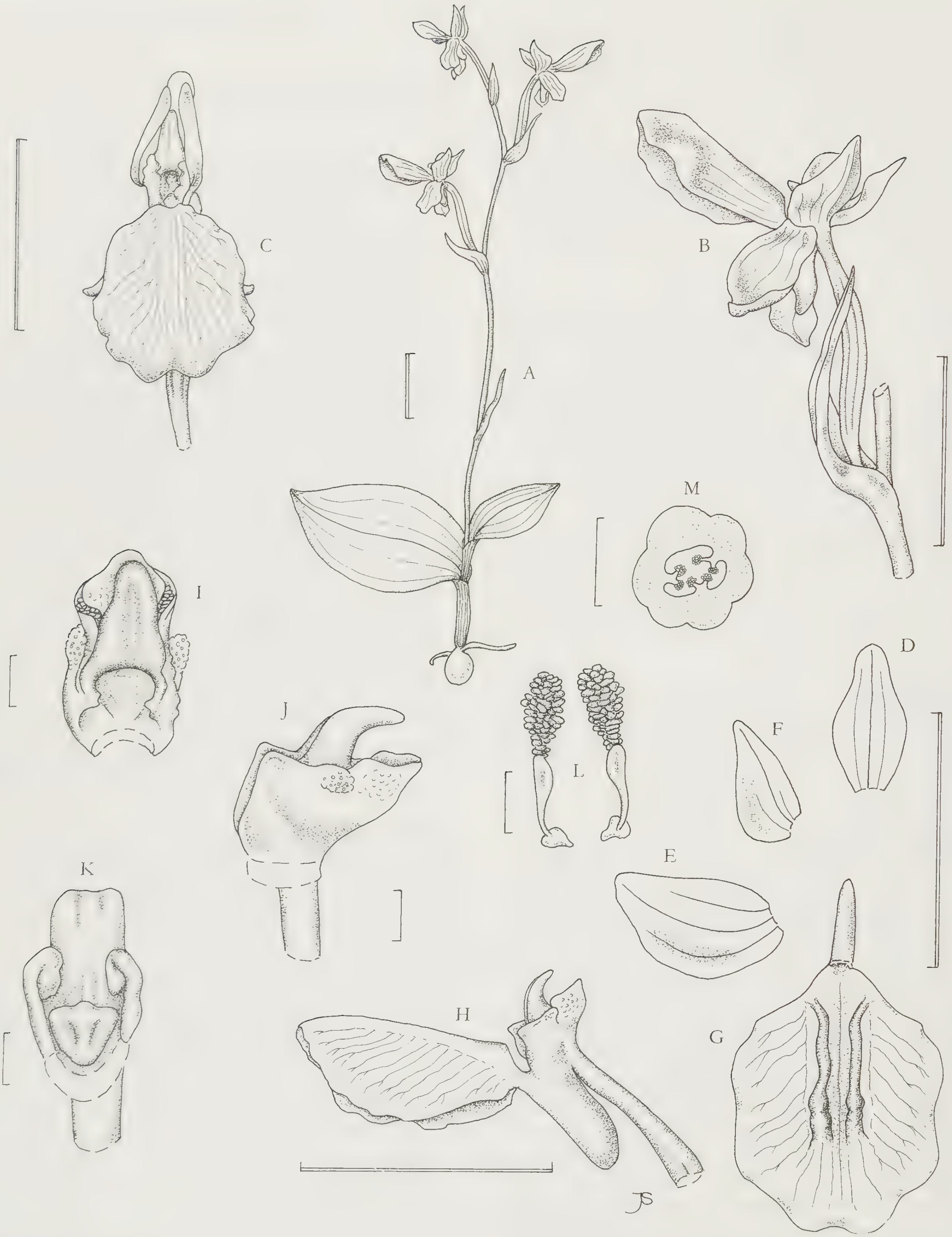

Fig. 79.1. *Hemipilia calophylla* Par. & Rchb.f. A. Habit; B. Flower, side view; C. Flower, front view; D. Dorsal sepal; E. Lateral sepal; F. Petal. G. Labellum; H. Labellum and column, side view; I. Column, from above; J. Column, side view; K. Column, front view; L. Pollinaria; M. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Henry 12472* (K) and Kew Spirit Collection no. 5885.

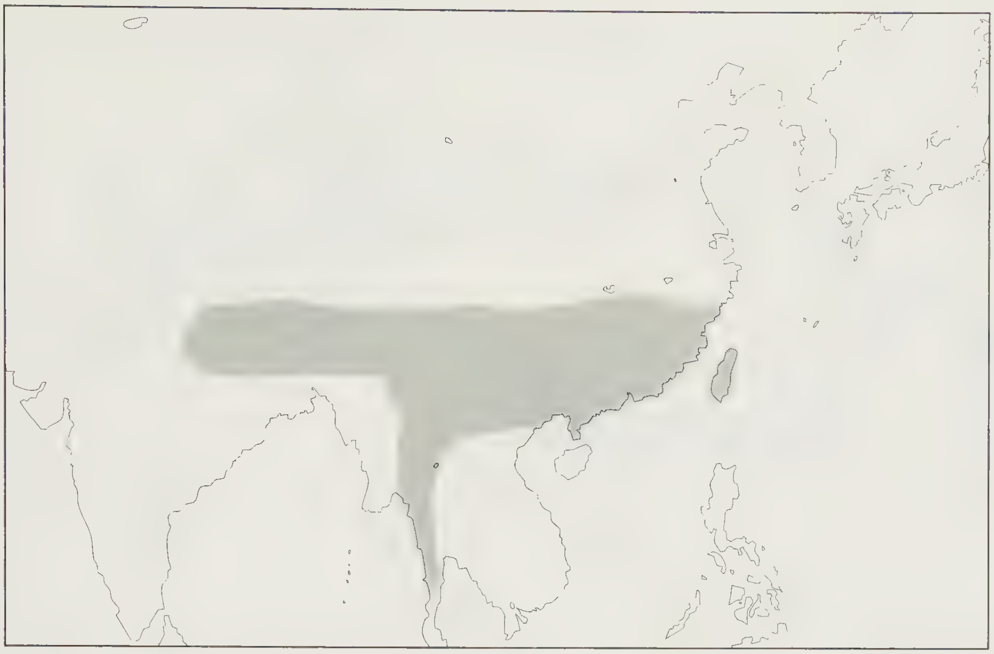

Fig. 79.2. Distribution map of *Hemipilia.*

Distribution (Fig. 79.2)

A small genus of possibly ten species distributed in northern India, Nepal, Bhutan, northern Myanmar (Burma), Thailand, and southern and western China, including south-eastern Xizang and Taiwan. **(PC)**

Ecology

Species of *Hemipilia* grow at high elevations, from 800–3500 m (Chen and Tang 1982). *Hemipilia cordifolia*, for example, has been reported as occurring in the high mountains of western temperate Himalaya from Mussourie to Nepal (Hara *et al.* 1978), flowering in August. Plants occur in rocky, humus-rich places in open forest, forest margins, rock-crevices, road sides, and on grassy slopes, usually on alkaline limestone soils. *Hemipilia calophylla* was reported growing on limestone rocks in northern India (Hooker 1894). **(RN, PC)**

Uses

None recorded. **(PC)**

Cultivation

These should be treated as woodland plants. Compost D. **(CB)**

Taxonomic notes

Hemipilia may be distinguished from *Ponerorchis* by its solitary, fleshy leaf appressed to the substrate and flowers with a long spur, divergent anther loculi, and a characteristic rostellum with a large porrect rather prominent mid-lobe, and incurved side lobes that partially cup the viscidia. **(PC)**

80. HERMINIUM

Herminium L., *Opera Varia*, 251 (1758); R.Br. in Aiton, *Hort. Kew.* ed. 2, **5**, 191 (1813). Type species: *H. monorchis* (L.) R.Br. (syn. *Ophrys monorchis* L.)

Monorchis Seguier, *Fl. Veron.* **3**, 251 (1754). Type species: *Ophrys monorchis* L.

Aopla Lindl., *Bot. Reg*, sub t. 1701 (1834). Type species: *Aopla reniformis* Lindl.

Derivation of name

Two suggestions have been offered for the derivation of this name: either that it is derived from the Greek *hermin*, a bed-post, possibly descriptive of the two knob-like staminodia that stand on each side of the anther or to the tubers, both of which fancifully resemble a carved bed-post, or that it is named for the Greek god Hermes, the God of trade and thieves. The first seems the more likely. **(PC)**

Description (Plate 100; Fig. 80.1)

Small, terrestrial, glabrous *herbs* with oblong, undivided tubers. *Leaves* solitary or few, green. *Inflorescence* erect, laxly to densely many-flowered; bracts small, lanceolate. *Flowers* small, often spidery, yellow or green. *Sepals* subequal, dorsal free or connivent into a hood, the laterals spreading. *Petals* smaller than the sepals, often connivent with dorsal sepal to form a hood over the column. *Labellum* continuous with the column base, spreading or pendulous, entire, bilobed or trilobed, flat, concave or obscurely saccate at the base, ecallose. *Column* short; anther bilocular, adnate to the face of the column; loculi parallel; pollinia two, with short caudicles; viscidia two, small to large; lateral appendages prominent, sometimes shortly stalked; stigma bilobed, convex, clavate; rostellum short. *Ovary* sessile. **(PC)**

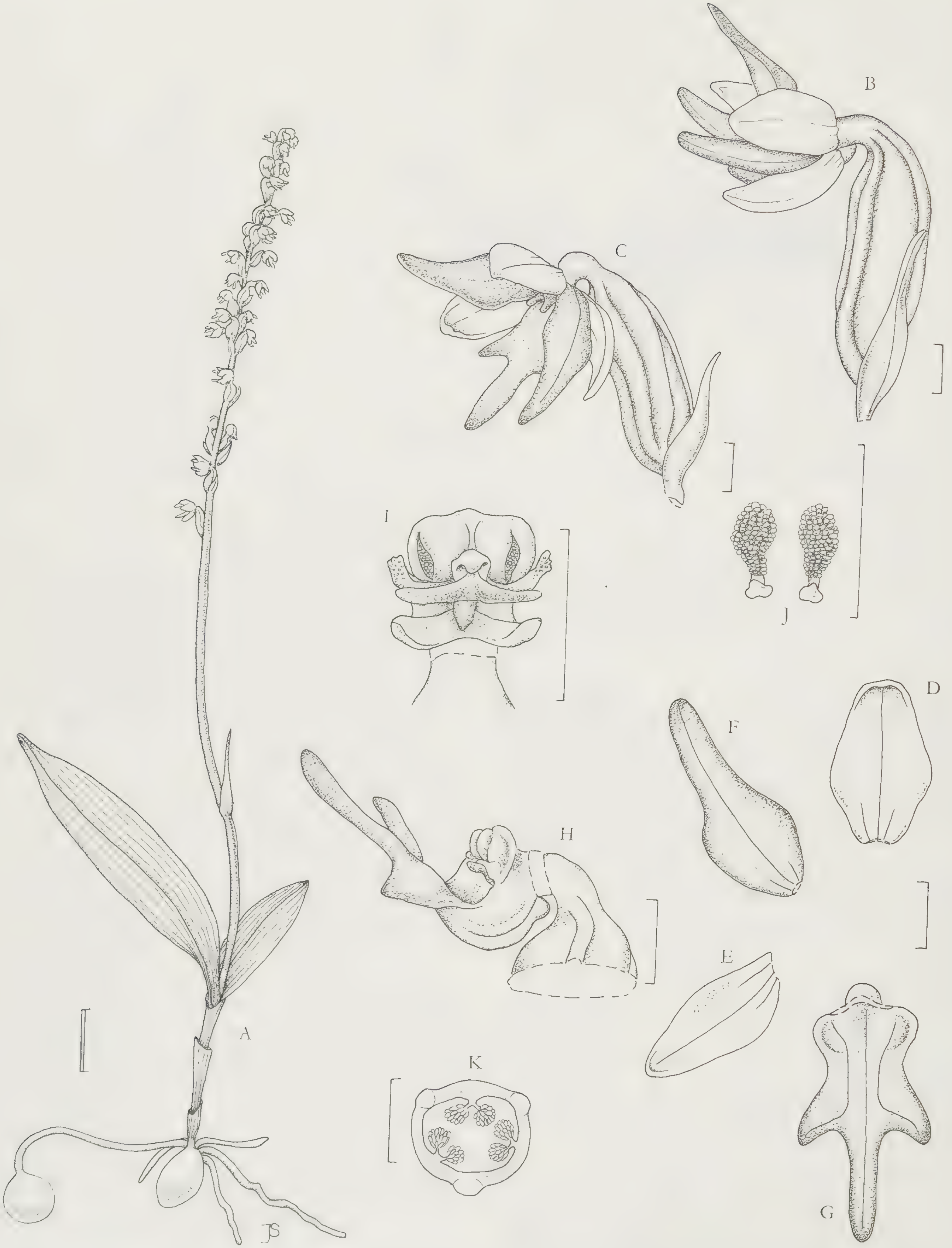

Fig. 80.1. *Herminium monorchis* R.Br. A. Habit; B. Flower, side view; C. Flower, oblique view; D. Dorsal sepal; E. Lateral sepal; F. Petal; G. Labellum; H. Labellum and column, side view; I. Column, front view; J. Pollinaria; K. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Willmot s.n.* (K) and Kew Spirit Collection no. 31601.

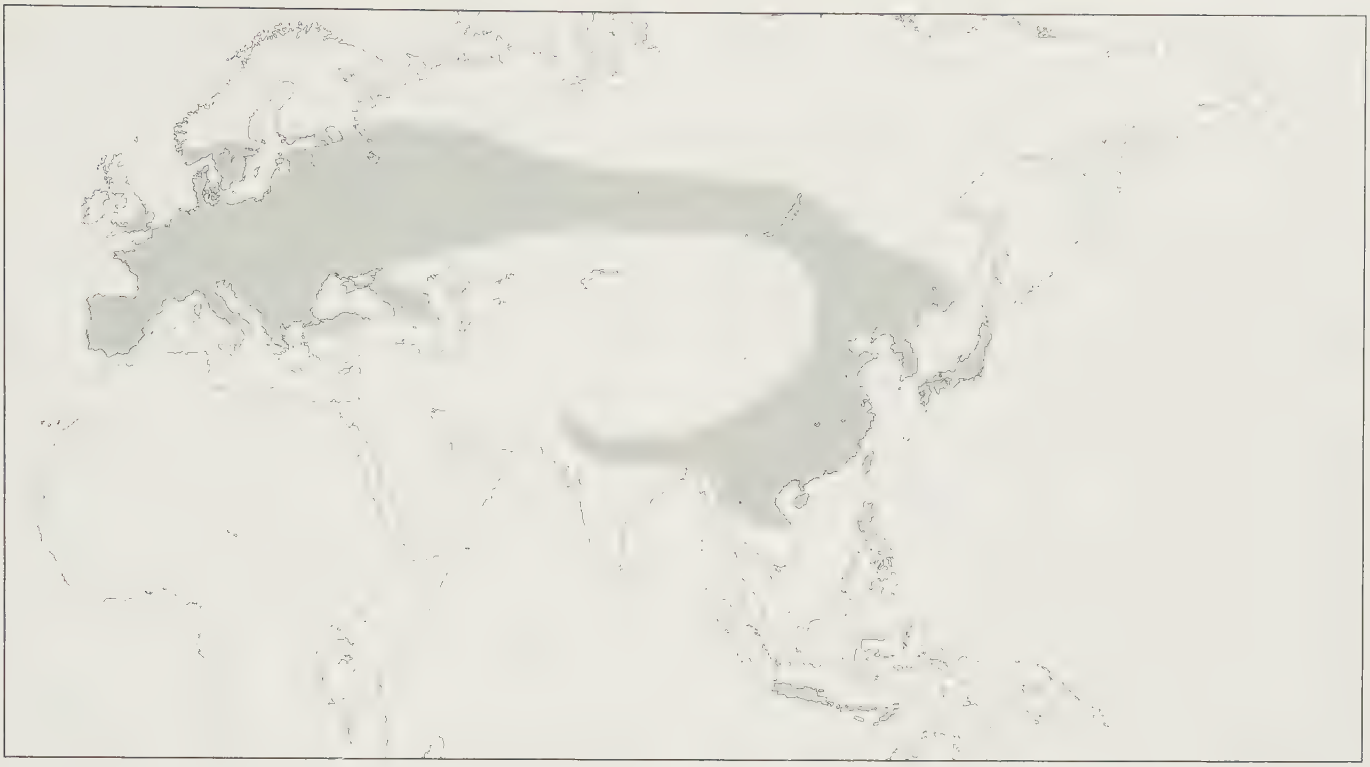

Fig. 80.2. Distribution map of *Herminium*.

Distribution (Fig. 80.2)

A genus of about 30 species widely distributed in Europe, North Africa, the Middle East and Asia to Japan, China, including Taiwan, and south to the Himalayas from Pakistan eastward, south-east Asia, the Philippines, and Indonesia. **(PC)**

Cytogenetics

In the genus *Herminium* the basic numbers are x = 19 and x = 20. Within the framework of chromosome numbers presented in Table C.2, it seems likely that the basic number x = 19 originated from x = 20 through a dysploid reduction. **(SD)**

Phytochemistry

Glucomannans have been detected in the tubers of *Herminium angustifolium* Benth. (Ohtsuki 1937). This study was carried out as part of a survey of the constituents of the tubers of a number of Japanese orchid species. **(NV, RG)**

Ecology

Species of *Herminium* typically grow in calcareous to neutral soils (Davies *et al.* 1988; Delforge 1995). In the British Isles, for example, *H. monorchis* R.Br. is principally found on the chalk downland of Kent, Sussex, Surrey, Hampshire, Wiltshire, and the Chilterns in the south of England and on the oolitic limestone of Somerset and Gloucestershire in the west of the country (Summerhayes 1951; Lang 1989). It normally grows in short grass such as among the short turf of the chalk downs, old pastures, old quarries, and on the spoil-heaps of ancient chalk-pits (Summerhayes 1951; Lang 1989; Sanford 1991; Wells *et al.* 1998). In the Cotswolds, *H. monorchis* is particularly abundant on bare quarry floors, and Lang (1989) reported it persisting in an old chalk pit in Kent more than 100 years after it was first recorded there in 1871. Wells *et al.* studied a population of *H. monorchis* between 1966 and 1995 that grows in species-rich chalk grassland (CG5 in the National Vegetation Classification, Rodwell 1993) that had developed over old quarry spoil (Wells 1981; Wells *et al.* 1998). The site, at Tottenhoe Knolls in Bedfordshire, is maintained in a short and open condition by scrub removal, winter sheep grazing, and high levels of rabbit herbivory.

Since it invariably grows in open habitats such as those at Tottenhoe Knolls, *H. monorchis* is thought to be intolerant of shade in Britain but is able to withstand some levels of drought as many of its sites in England can become dry in the summer (Summerhayes 1951). Outside the United Kingdom, *H. monorchis* often grows in both wetter and more shaded habitats, as do other members of the genus. *Herminium* species are recorded from coastal sand-dune slacks, marshes, and damp meadows (Davies *et al.* 1988; Delforge 1995), shrubby vegetation (Dassanayake 1981) and forests and marshy ground (Dassanayake 1981) as well as from fields, roadsides, and grasslands elsewhere in Asia (Ohwi 1965; Walker 1976). *Herminium* can grow at a range of elevations from sea level in the northern parts of its range as in Britain (Summerhayes 1951) up to 2400 m in moutainous areas in Europe (Delforge 1995), and at even higher elevations in the Himalayas (Hara *et al.* 1978). Indeed, in his *Flora of British India*, Hooker (1894) noted that 'the Indian *Herminia* are all mountain or alpine, and attain the greatest elevation of any orchids'.

Across its geographic range, *Herminium* flowers between May and August, the exact period depending on the elevation of the population (Dassanyake 1981; Davies *et al.* 1988; Delforge 1995). Peak flowering of *H. monorchis* in England, for example, is normally in the last two weeks of June and the first two weeks of July (Summerhayes 1986; Lang 1989; Sanford 1991; Wells 1998). Flowering of this species is preceded by leaf expansion, the leaves emerging from below ground in either May or June depending on whether there has been sufficient rainfall to promote early growth (Wells *et al.* 1998). In normal years, the leaves are green until mid-September, but if there is a summer drought, they remain small and turn yellow so that they are unable to photosynthesize by mid-summer. Adverse weather conditions such as drought or high summer temperatures are thought to influence patterns of flowering in *H. monorchis* at least. Flowering of this species is often described as being highly variable, with marked fluctuations being seen in the number of flowering stems produced by populations from year to year (Summerhayes 1951; Lang 1989; Delforge 1995). In the long-term study population of *H. monorchis* at Tottenhoe Knolls in England, for example, the average proportion of flowering plants was 16.9%, but this varied from 0 in 1977 and 1991 to 36% in 1972 (Wells *et al.* 1998). By causing premature senescence of the leaves, unusually warm and dry seasons reduce the amount of carbohydrates that can be produced and stored by a plant with the result that the subsequently smaller tubers are unable to initiate inflorescence formation the following year (Wells 1998). *Herminium monorchis* seems to be particularly sensitive to climatic variations during its period of active growth (June to October), but its tubers enable it to survive in a dormant state during unfavourable conditions. Wells *et al.* (1998) noted that the population at Tottenhoe was able to maintain itself solely by vegetative means because from 1990–1995 all inflorescences (77 in that period) were grazed by rabbits, and there had been no fresh seed input to the site for five years.

Fruit-set in *H. monorchis* is normally high, for example 88.7% in one population in Sweden (Nilsson 1979), and has been attributed by several authors to a high degree of self-pollination even in the absence of pollinators (e.g. Summerhayes 1951; Lang 1989). However, Nilsson (1979) demonstrated that insects were necessary for pollen transport in the species because no fruit was set if inflorescences were experimentally isolated throughout anthesis as pollinia did not come into contact with the stigma without the intervention of a pollen vector. Seedlings are rarely observed in the field (Rasmussen 1995), which has led to the suggestion that propagation of the species is principally by vegetative means (Delforge 1995). Vegetative reproduction in *Herminium* is efficient because two or three additional new tubers are normally produced on stolons up to 20 cm long (Davies *et al.* 1988; Lang 1989). Given the consistent large input of seeds, it is probable that both vegetative and sexual reproduction contribute to the propagation of the species and formation of large colonies in the field of several thousand plants at some sites (Delforge 1995). Rasmussen (1995) observed low germination rates of seeds with *Rhizoctonia* fungi (3–13%) on nutrient media, but asymbiotically cultured protocorms grew well, and flowering plants could be obtained within two years after sowing. Earlier observations also indicated that *H. monorchis* requires a period of several years before reaching flowering size under natural conditions and that the tip of the tuber is mycorrhizal, whereas fungi are absent from other underground parts of the plant (Fuchs and Ziegenspeck 1925, cited in Rasmussen 1995).

Despite its high seed productivity and efficient means of vegetative propagation, which can make it abundant at favourable sites, *H. monorchis* has a localized distribution in the UK and in other temperate and boreal areas. Summerhayes (1951) suggested that the species, which is at the edge of its range in Britain, is restricted by climatic variables. It avoids the western parts of the British Isles and continental Europe that have a damp oceanic climate. In recent years it has declined in numbers and is now uncommon (Davies *et al.* 1988), even in areas where it was previously common. For example, in Suffolk in south-east England it has been extinct for over 170 years. Sanford (1991) attributed its disappearance to changing agricultural practices in the region, whereby many open fields were ploughed up after 1800 to grow arable crops, and sheep grazing, which kept the grass short, was moved to other areas. He compared the decline of *H. monorchis* to that of *Ophrys fuciflora* in England and speculated that climatic changes could have been an important factor in the reduction of the occurrence of the species in England. It is also rare in other parts of its range such as Japan where it occurs in Hokkaido (Ohwi 1965). Other *Herminium* species reported as rare include *H. forrestii* Schltr. in China (Cribb 1994) and *H. longicrure* Benth. & Hook.f in Japan (Ohwi 1965). Pradhan (IUCN Orchid Specialist Group 1996) listed the Indian endemic species, *H. kalimpongensis* U. C. Pradhan, as the most threatened orchid species of the country because it has not been recorded for a long time. Other members of the genus are common in parts of the range of the genus: *H. lanceum* (Thunb. ex Sw.) Vuijk in south-east Asia, Pakistan to south-west China (Polunin and Stainton 1984) and *H. monorchis* and *H. ophioglossoides* Schltr. in Yunnan in China (Cribb 1994). **(RN)**

Uses

Herminium monorchis is used in herbal medicine in China as a general tonic (Chen and Tang 1982). **(RN)**

Cultivation

Compost C and D. **(CB)**

Taxonomic notes

The circumscription of *Herminium* needs to be reconsidered. We exclude those Far Eastern species with a long spur, which probably belong in *Peristylus*. *Herminium* is close to *Androcorys*, and some of the species with an entire lip and saccate base that are currently included in *Herminium* may be better placed in an expanded *Androcorys*. **(PC)**

81. HIMANTOGLOSSUM

Himantoglossum (L.) W. D. J. Koch, *Syn. Fl. Germ. Helv.*, 689 (1837). Type species: *Himantoglossum hircinum* (L.) Rich.

Loroglossum Rich., *Orch. Eur. Annot.*, 32 (1817). Type species: *Loroglossum hircinum* (L.) Rich.

Derivation of name

From the Greek *himas*, *himantos*, strap, and *glossa*, tongue, referring to the characteristic mid-lobe of the lip. **(JW)**

Description (Plate 101; Fig. 81.1)

Robust *herbs. Rootstock* tuberous, tubers large, ovoid or ovate-oblong, entire. *Stem* erect, leafy, glabrous. *Leaves* often large, oblong-ligulate, unspotted. *Inflorescence* densely or laxly many-flowered, broad; floral bracts membranous, equalling or shorter than floral hood. *Flowers* large, greenish to purplish. *Sepals* and *petals* connivent to form an obtuse hood. Petals narrow. *Labellum* spurred, three-lobed, much longer than hood, side lobes short, obliquely linear to triangular-falcate, margins undulate, mid-lobe long, linear, strap-shaped, often deeply bifurcate and spirally twisted. *Column* short; rostellum prominent, lamellate; stigmatic cavity quadrate to circular, shiny; lateral appendages small, verrucose; anther obtuse; pollinia two, caudicles attached to a single viscidium, enclosed in a large, hemispherical bursicle. *Ovary* sessile, twisted. **(JW)**

Distribution (Fig. 81.2)

Four species distributed in western, central, and southern Europe and North Africa, eastwards to Turkey, the Caucasus, and south-west Iran. **(JW)**

Palynology

In three species of *Himantoglossum* examined, Schill and Pfeiffer (1977) reported verrucose-hamulate sculpturing. In the case of *H. hircinum*, there are sculptural differences between the lateral and frontal portions of the same massula, distinctly verrucose-hamulate on the sides but coalescing into gemmae of different sizes on on the front. **(AP)**

Cytogenetics

According to reports available in the literature, *Himantoglossum* is represented by the diploid chromosome number $2n = 36$. However, cases of aneuploidy with $2n = 36 + 1B$ are also known in both *H. hircinum* and *H. adriaticum* (Capineri and Rossi 1987; D'Emerico *et al.* 1993). The two species studied have similar karyotypes with mainly metacentric chromosomes (D'Emerico *et al.* 1990; 1993). These close karyological resemblances may indicate that the two species are closely related. Neither these two species have stainable heterochromatin, at least in the populations analysed.

From a detailed comparison of the karyotypes of *H. hircinum*, *H. adriaticum*, and *Barlia robertiana*, it is apparent that the species have a low asymmetrical karyotype and banding properties similar to those of the *Anacamptis morio* group (Fig. C.3). **(SD)**

Phytochemistry

Infection of the tubers of *H. hircinum* with a strain of *Rhizoctonia repens* from *Orchis militaris* results in the synthesis of the phytoalexin orchinol (2,4-dimethoxy-7-hydroxy-9,10-dihydrophenanthrene) and *p*-hydroxybenzylalcohol. This observation was made as part of a survey of orchinol and *p*-hydroxybenzylalcohol production in a number of species representing genera in subtribe Orchidinae (Nüesch 1963; Gaumann *et al.* 1960). An isomer of orchinol, 2,4-dimethoxy-5-hydroxy-9,10-dihydrophenanthrene (loroglossol) was reported at levels of approximately 150 mg kg^{-1} in *H. hircinum* tubers infected with *R. versicolor* (Hardegger *et al.* 1963; Urech *et al.* 1963). A related phytoalexin, 4-methoxy-2,5-dihydroxy-9,10-dihydrophenanthrene (hircinol), also occurs in the same source at higher concentrations (250–400 mg kg^{-1}) than those found for loroglossol. The anti-fungal activity of orchinol and hircinol against *Candida lipolytica* (BY 17) has been assessed (Fisch *et al.* 1973). Orchinol was found to be more active than hircinol at both 50 ppm and 100 ppm and caused complete inhibition of growth of *C. lipolytica* for the first six days when applied at the latter concentration. Loroglossol was stated to be inactive in these assays. In a later report, the activity of loroglossol against spore germination of *Monilinia fructicola* (Wint.) Honey and *Phytophthora infestans* (Mont.) de Bary was described (Ward *et al.* 1975). The failure of this compound to show activity in earlier investigations was linked to its low solubility in water. Chemical structures of the three 9,10-dihydrophenanthrenes found in *Himantoglossum* and other Orchidinae are shown in Fig. 81.3.

A phenolic glucoside (loroglossin; also denoted loroglossine by some authors) was isolated as a crystalline substance from *H. hircinum* by Bourquelot and Bridel (1919), following their earlier observations on hydrolysable glucosides in a number of species of European terrestrial orchids (Bourquelot and Bridel 1914*a*,*b*). The structure of loroglossin (Fig. 81.4) was determined to be *bis*[4-(β-D-glucopyranosyloxy)benzyl] *erythro*isobutyltartrate by Aasen *et al.* (1975). In addition, Gray *et al.* (1976, 1977) showed that the configurations at C-2 and C-3 were (*R*) and (*S*), respectively.

The chemical composition of the scent of *H. hircinum* flowers was obtained by gas chromatography coupled with mass spectroscopy (Kaiser 1993). The principal components are (*E*)-3-methyl-4-decenoic acid, (*Z*)-4-decenoic acid and lauric acid. The anthocyanin content of the flowers of *H. adriaticum* was investigated by Strack *et al.* (1989) **(NV, RG)**

Ecology

Himantoglossum is confined to dry calcareous soils throughout its range. In southern England, for example, *H. hircinum* is primarily found growing on chalk downlands but also occurs in the limestone areas of Gloucestershire and Oxfordshire and has been recorded from the sandy soils of stabilized sand-dunes in England, Holland, and France (Summerhayes 1951).

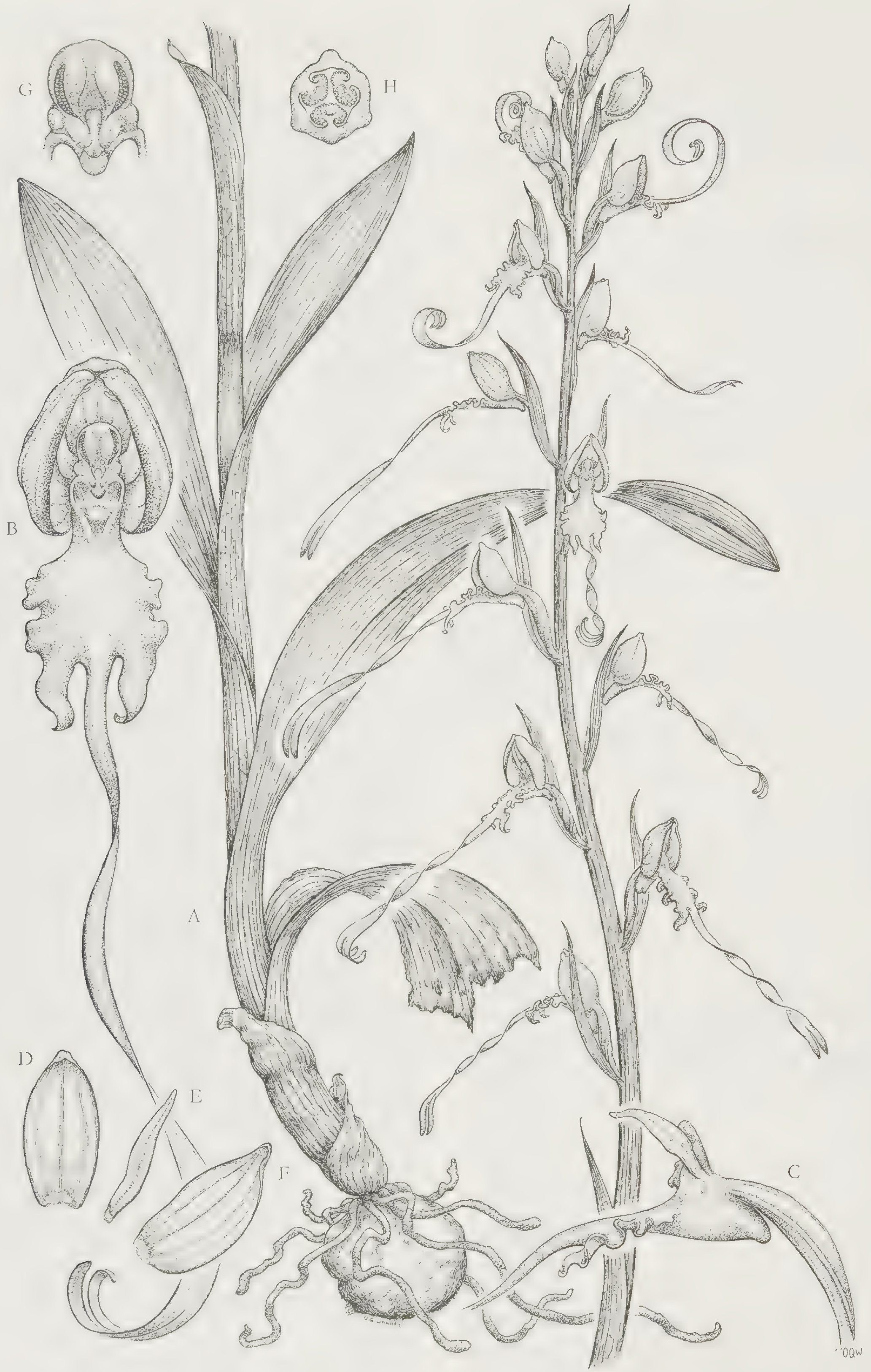

Fig. 81.1. *Himantoglossum affine* Schltr. A. Habit, ×1; B. Flower from front, ×3; C. Flower from side, sepals removed, ×3; D. Dorsal sepal, ×3; E. Petal, ×3; F. Lateral sepal, ×3; G. Column apex, ×6; H. Ovary, transverse section, ×6. Drawn by Oliver Q. Whalley from Kew Spirit Collection no. 47948.

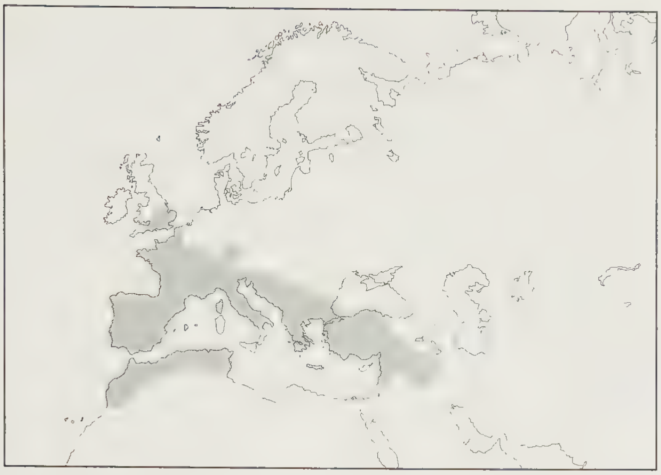

Fig. 81.2. Distribution map of *Himantoglossum.*

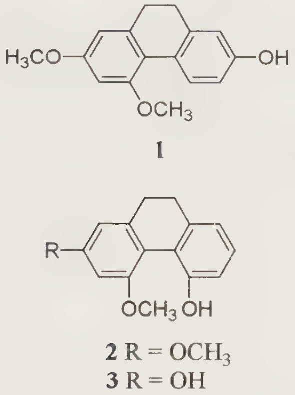

Fig. 81.3. 9, 10-Dihydrophenanthrenes of *Himantoglossum* and other Orchidinae. (**1**) orchinol, (**2**) loroglossol, (**3**) hircinol.

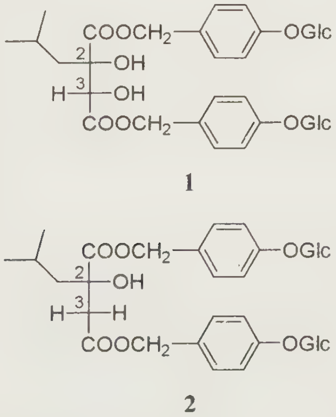

Fig. 81.4. Phenolic glycosides of *Himantoglossum* and other Orchidinae. (**1**) loroglossin, (**2**) militarine. The structures are shown in the Fischer representation. Glc = β-D-glucopyranosyl.

Himantoglossum normally grows in full sun to semi-shade in grassland, meadows, shrubland, garrigue, rough hillside pastures, and open woodlands comprising oak, juniper, or pine (Delforge 1995). Members of the genus are also frequently found growing in disturbed habitats such as railway embankments, roadside verges, and chalk pits (Davies *et al.* 1988; Rasmussen 1995). In habitats with scrub and tall grass (such as some English downlands) orchids that frequently co-occur with *Himantoglossum* are *Gymnadenia conopsea, Dactylorhiza fuchsii,* and *Anacamptis pyramidalis* (Summerhayes 1951). On stabilized sand-dunes it is often accompanied by *Anacamptis pyramidalis* and *Allium oleraceum* L. (Alliaceae; Lang 1989). In addition to growing at sea level in coastal locations, *Himantoglossum* also occurs in mountainous areas at elevations of up to 1800 m (Delforge 1995).

Plants flower in different parts of the range between April and August. For example, *H. hircinum* starts to flower in April in southern Europe, whereas in Britain it flowers in the summer in late June to early July. At the time of flowering, the lower leaves have usually withered as their water was utilized in the expansion of the inflorescence in the spring (Summerhayes 1951; Davies *et al.* 1988; Lang 1989). These leaves were formed in the previous autumn and remained green throughout the winter ('winter-green'). Following flowering and fruit-set, the whole plant senesces and survives underground as a tuber. Mycotrophic roots develop from the tuber in the autumn prior to the re-appearance of the aerial stem in the winter (Fuchs and Ziegenspeck 1925, cited in Rasmussen 1995).

Fruit-set levels of up to 30% are reported for *H. hircinum* (Lang 1989), and even solitary plants usually set some fruits (Summerhayes 1951). However, fruit-set varies from year to year, as recently demonstrated by a study population in Kent in southern England (Carey 1998). In 1994 each plant produced at least five capsules, but in the following year most inflorescences failed or aborted before pollination such that few fruits were produced. It has been estimated that each capsule of *H. hircinum* contains about 1200 seeds (Summerhayes 1951). Lang (1989) suggested that seed production is an important means by which the plant has spread across England. At the local level, Carey (1998) also attributed the marked spread of *H. hircinum* at a site in Kent in southern England over a 20-year period to seed dispersal.

Germination of *Himantoglossum* seeds and development of a protocorm probably occurs rapidly in the field, that is by the autumn following seed dispersal (Ziegenspeck 1936, cited in Rasmussen 1995). The first tuber is formed from a bud in the axil of a scale leaf at the tip of the protocorm during the first spring after seed germination. At the tip of the tuber, a short rhizome with roots develops in the second autumn, and a second tuber begins to grow, which reaches full size in the early summer. The rhizome and roots are mycotrophic and may be infected with a diverse range of endophytes. For example Gäumann *et al.* 1961 (cited in Rasmussen 1995) isolated 15 fungi from the roots of *H. hircinum*, 14 of which were identified as Ascomycetes and one as *Rhizoctonia versicolor*. The only part of the plant to survive the summer resting period is the second tuber, as the rhizome, roots, and first tuber have senesced by that time. The annual underground cycle of rhizome, root, and tuber development is repeated again for at least another year before the first leafy stem emerges above the ground, such that newly emerged plants in any population of *Himantoglossum* are at least two years old (Ziegenspeck 1936, cited in Rasmussen 1995). Seedling establishment and maturation of the tuber are influenced in different ways by summer weather conditions. Whereas high precipitation levels in the summer promote establishment of *Himantoglossum* seedlings, they have an adverse effect on tubers, sometimes causing them to rot and thus may lead to the death of mature *Himantoglossum* plants following flowering (Vöth 1980, cited in Rasmussen 1995).

Throughout its range *Himantoglossum* is usually local and rare. Even the most widespread species, *H. hircinum*, is rare throughout most of the Mediterranean (Davies *et al.* 1988; Summerhayes 1951) with a localized occurrence in north Africa and absence from southern Italy (Delforge 1995). It is most abundant in western France, where it can sometimes be found in large numbers, probably because of its apparent preference for an oceanic climate (Summerhayes 1951). Similarly, the other species in the genus are all locally distributed and in most cases also rare (Davies *et al.* 1988). The only species that occurs in the UK is *H. hircinum* where, as in much of the rest of Europe, it is rare and sporadic in its occurrence. In most cases, only solitary plants are found, but sometimes larger populations have been recorded such as one population of over 200 plants in Kent (Summerhayes 1951). They can be unpredictable in their appearance above ground and inexplicably disappear after flowering successfully for a number of years in succession (Davies *et al.* 1988; Lang 1989).

The history of the distribution of *H. hircinum* in Britain is unusual compared to that of other British orchids, most of which have shown a marked decrease in occurrence in recent years (Hutchings 1989). The earliest record of *H. hircinum* is from 1641 for several localities around Dartford and Crayford in Kent. These populations persisted for the next 200 years, but in about 1850 the species died out in the area (Summerhayes 1951; Lang 1989). During the latter half of the 19th century, *H. hircinum* was found in an additional 20 localities in south-east England, mostly on the North Downs in Kent, Suffolk, and Hampshire. Because these were small and short-lived populations, it was still considered an extremely rare species in England and threatened with extinction from the British Isles. At the beginning of the 20th century, however, the frequency of occurrence of *H. hircinum* began to increase. Between 1900 and 1933, another 129 stations were found including sites well outside its previous limits in south-east England, as far north as Yorkshire and as far west as Devon. Although many were for single plants that failed to persist for more than one or two years (Perring 1974), this still represented a considerable increase in the spread of the species throughout England, which Good (1936) explained as the result of an alteration in climatic conditions. Meterological records showed that between 1900 and 1933 the climate became more equable, slightly warmer in winter and cooler in summer than prior to 1900. Good suggested that this change toward a more oceanic type of climate, such as that encountered in western France, allowed the species to grow in greater numbers and spread to a wider variety of sites throughout England (although in recent years doubts have been cast as to the likelihood of this explanation, which has never been tested experimentally; Willems 1982). A sensitivity of *H. hircinum* to changes in climatic conditions might also explain why the English distribution of the species has declined since the 1940s such that it was reduced to just nine sites (Perring 1974) and today is a Red Data Book species.

In Britain and elsewhere in its distribution *Himantoglossum* is also susceptible to human disturbance. One possible explanation for the disappearance of some populations is excessive gathering by collectors (Summerhayes 1951). One colony that had flourished in Bedfordshire between 1938 and 1947 was subsequently destroyed by ploughing (Lang 1989). In Turkey, *Himantoglossum* is threatened by collection for production of ice cream (Delforge 1995). **(RN)**

Pollination

Detailed studies of the pollinators of the spectacular flowers of *Himantoglossum* were made by Teschner (1980) and Vöth (1990). They agreed that the main pollinators are bees. Teschner (1980) suggested that solitary bees such as *Andrena* and *Colletes* are the original pollinators of *Himantoglossum*. He found evidence for the presence of glucose in the spur of most flowers, and spurs often seem moist, indicating that small quantities of nectar are present. However, Vöth (1990) found no evidence for nectar in the spur but rather on the papillae at the spur entrance. This nectar could be exploited by small, short-tongued pollinators but not by long-tongued ones such as *Apis*, which search for nectar in the spur. It may be that *Himantoglossum* was originally adapted to short-tongued pollinators but shifted to *Apis* because short-tongued pollinators have become rare, especially in the northern part of its current distribution, and *Apis* has taken over the role of the pollinators. Vöth (1990) further suggested that the papillae at the spur entrance mimic the presence of pollen, which is of major interest to visiting *Colletes* spp. **(AW, SC, AD)**

Uses

Plants are collected for production of salep and a sticky ice cream in southern Turkey. **(PC).**

Cultivation

Like most other species of Orchidinae, plants grow in calcareous grassland and should be cultivated in compost C with added lime. Good (1936) noted that mature plants removed from the field and brought into cultivation usually diminished in size after some years or died in the first flowering season. **(CB)**

Taxonomic literature

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82. HOLOTHRIX

Holothrix Lindl., *Gen. Sp. Orch. Pl.*, 257, 283 (1835), *nom. cons.* Type species: *H. hispidula* (L.f.) Th. Dur. & Schinz, *typ. cons.*

Monotris Lindl., *Bot. Reg.*, 19 ad t. 1701 (1834). Type species: *M. secunda* Lindl.

Scopularia Lindl., *Bot. Reg.*, 19 ad t. 1701 (1834). Type species: *S. burchellii* Lindl.

Saccidium Lindl., *Gen. Sp. Orch. Pl.*, 258 (1835). Type species: *S. pilosum* Lindl.

Tryphia Lindl., *Bot. Reg.* 19 ad t. 1701 (1834). Type species: *T. secunda* (Thunb.) Lindl.

Bucculina Lindl., in Hook., *Comp. Bot. Mag.*, **2**, 209 (1836). Type species: *B. aspera* Lindl.

Deroemera Rchb.f., *De Poll. Orch.*, 29 (1852). Type species: *D. squammata* (Hochst. ex A. Rich.) Rchb.f.

Derivation of name

From the Greek *holos*, whole, and *thrix* (*trichos*), hair, from the hairy leaves, stems and sepals of the plant. **(PC)**

Description (Plate 102; Fig. 82.1)

Terrestrial *herbs* with small, ovoid or ellipsoid tubers. *Leaves* radical, 1–2, appressed to ground, sessile, ovate or orbicular, sometimes withered by flowering time. *Inflorescence* erect, unbranched, with or without sheaths, sparsely to densely flowered. *Flowers* sessile or shortly stalked, often secund. *Sepals* subequal, free, sometimes setose, often hairy, usually green. *Petals* usually longer (often much longer) than sepals, entire or lobed, often rather fleshy. *Labellum* lobed or toothed, rarely entire, spurred; adnate to column at base. *Column* short; anther loculi parallel; pollinia two, granular; caudicles short; viscidia small, naked; stigma sessile. **(PC)**

Distribution (Fig. 82.2)

A genus of 50–60 species in tropical Africa, South Africa, and tropical Arabia. **(PC)**

Ecology

Members of the terrestrial genus *Holothrix* grow in a variety of habitats across its range in both exposed and shaded conditions. For example, the distribution of the 25 *Holothrix* species from South Africa encompasses the semi-arid regions of the Karoo and Namaqualand and the winter-rainfall area of the south-western Cape Province, to the forests and grasslands in the summer-rainfall areas of the eastern Cape Province, Natal, and the Transvaal (Schelpe 1966). In other areas such as Zambia, Malawi, and Tanzania, *Holothrix* is typically found in *Brachystegia* (Fabaceae) woodland and in dry grassland in the submontane or montane zones at elevations ranging from 1300–2300 m, where it often appears after the grass has been burned (la Croix and Cribb 1995). Plants are frequently located near boulders or among rocky areas that offer some shade or are sites of water seepage. In southern Africa *H. orthoceras* Rchb.f. is said to be often found among moss-covered rocks, *H. macowania* Rchb.f. in shallow soils near granite boulders, and *H. johnstonii* Rolfe and *H. longiflora* Rolfe on slabs of rock and in crevices in seepage slopes (la Croix and Cribb 1995). In Saudi Arabia, *H. arachnoidea* Rchb.f., which is widespread along the escarpment in the Asir and southern Hijaz, always occurs in shade, including the shade of boulders (Collenette 1985).

The main flowering season for *Holothrix* is the spring and summer. Prior to flowering, the slender stem and pair of leaves that typically lie flat to the ground arise from the small ovoid or ellipsoid underground tubers. Although the leaves usually do not senesce before the flowers open, this does occur in some species such as *H. thodei* Rolfe (Schelpe 1966). The formation of fruits in *Holothrix* has been recorded from some herbarium specimens collected from southern Africa (la Croix and Cribb 1995). **(RN)**

Uses

None recorded. **(PC)**

Cultivation

Many species grow in dry areas, scrub, or rocky outcrops. Compost C and E. (**CB**)

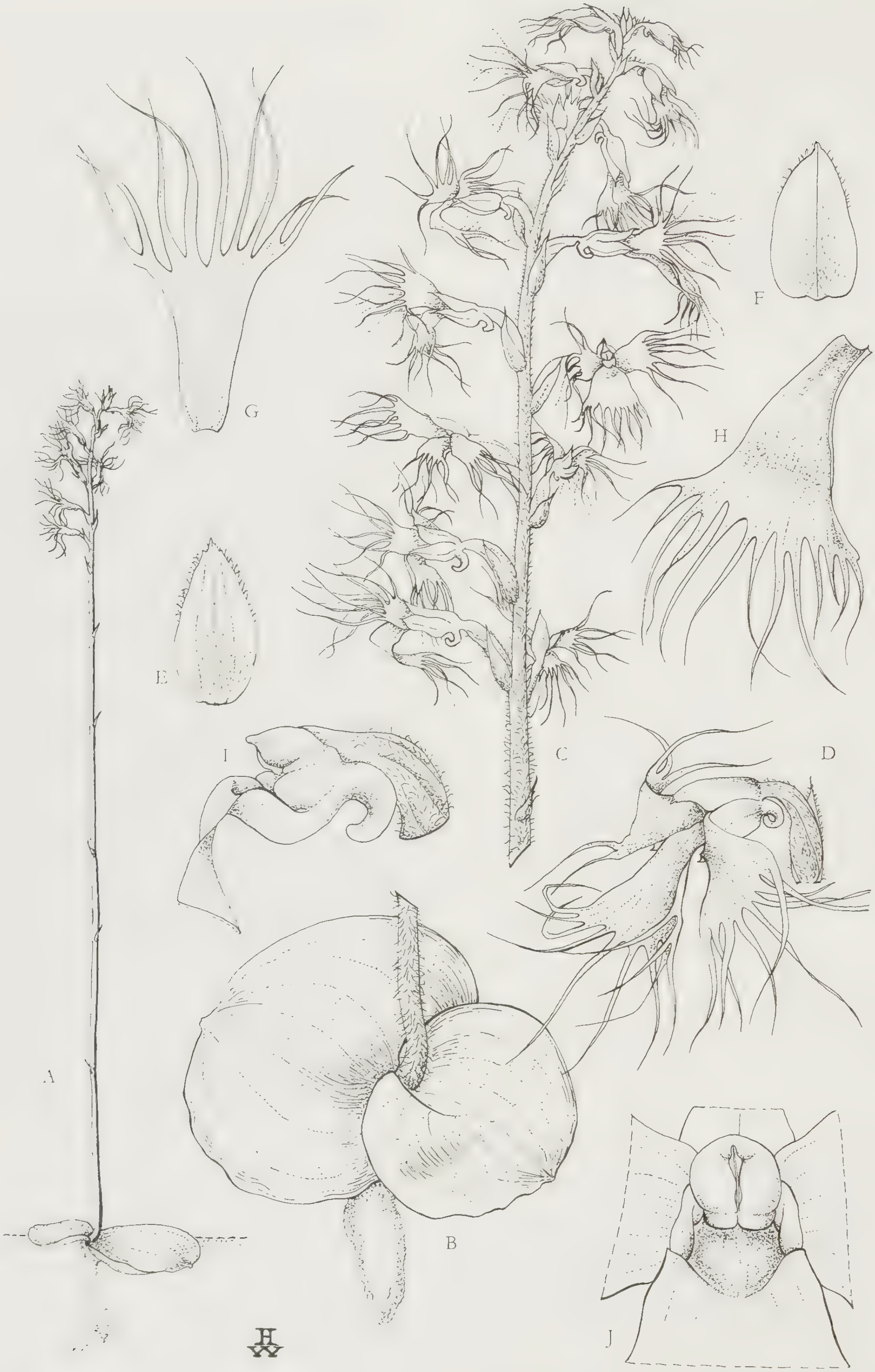

Fig. 82.1. *Holothrix longiflora* Rolfe. A. Habit, × 0.33; B. Stem, base, ×1; C. Inflorescence apex, ×1; D. Flower, oblique view, ×2; E. Dorsal sepal, ×3; F. Lateral sepal, ×3; G. Petal, ×3; H. Labellum, ×3; I. Column, side view, sepals and petals removed, ×5; J. Column, front view, ×10. Drawn by Heather Wood from *Richards 12140*.

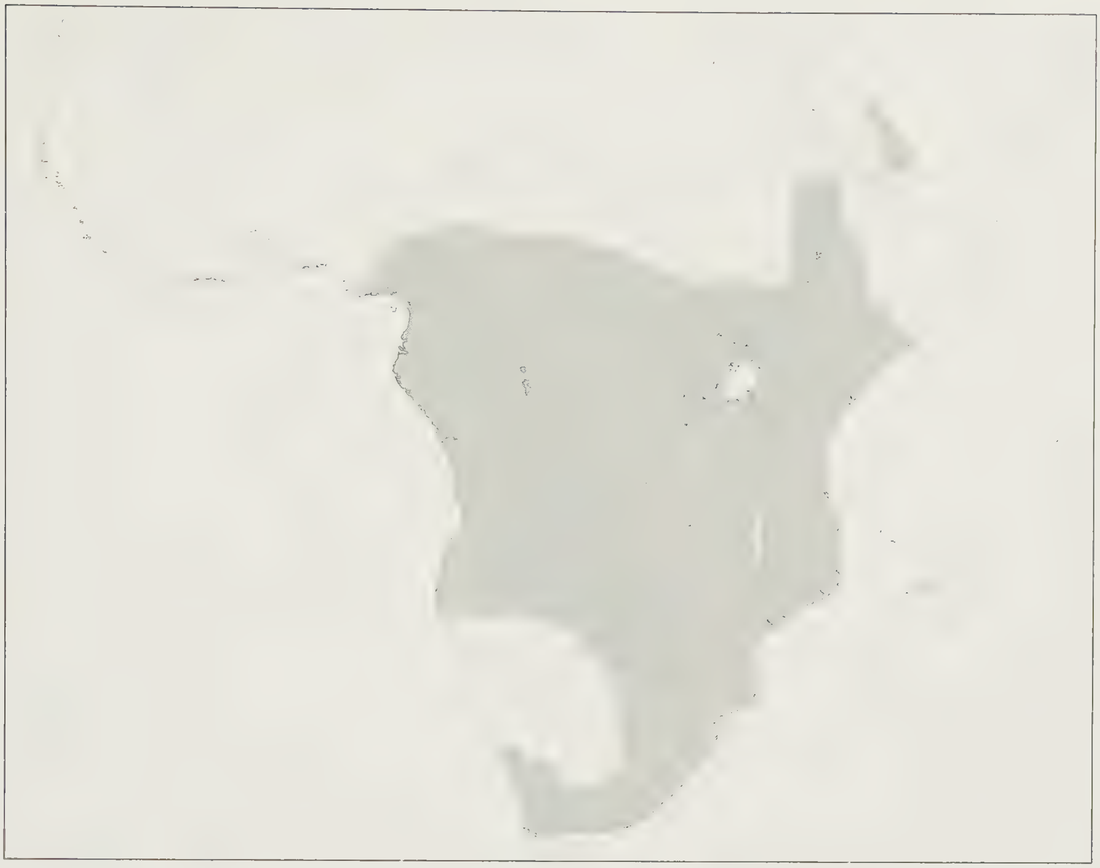

Fig. 82.2. Distribution map of *Holothrix*.

83. MEGALORCHIS

Megalorchis H. Perrier, *Bull. Soc. Bot. France*, **83**, 579 (1937). Type species: *M. regalis* (Schltr.) H. Perrier (syn. *Habenaria regalis* Schltr.)

Derivation of name

From the Greek *megas* or *megale*, great, and *orchis*, a testicle or orchid, in allusion to the large size of the plant and flowers. **(PC)**

Description (Fig. 83.1)

A large terrestrial *herb* with a stout leafy stem and fibrous roots fibrous; tubers not seen. *Leaves* many, elliptic-ligulate, acuminate, arranged spirally along the stem, smaller above, petiolate, green. *Inflorescence* terminal, densely many-flowered; bracts ovate-lanceolate, acuminate, longer than the pedicellate ovary. *Flowers* resupinate, large, white, glabrous. *Dorsal sepal* erect, free, ovate. *Lateral sepals* spreading-erect, free, falcate-ovate, dilated below, forming with the base of the labellum a large mentum. *Petals* entire, adnate to the dorsal sepal to form a hood over the column, obliquely ovate-triangular. *Labellum* large, porrect in basal half, recurved in apical half, three-lobed; side lobes erect; mid-lobe much larger, clawed, tongue-shaped, strongly recurved in middle; spur cylindrical, pendent. *Column* reclined, short and broad; rostellum three-lobed with a short low mid-lobe and two elongate, upcurved rostellar arms separated by a broad connective; pollinia two, clavate; viscidia two, large, cucullate; lateral appendages prominent. **(PC)**

Distribution (Fig. 83.2)

A monospecific genus endemic to the eastern mountains of central Madagascar. **(PC)**

Ecology

Megalorchis regalis is a terrestrial species that grows at elevations of 1800–2000 m in moss forest. It flowers in October–November (Du Puy *et al.* 1999). Habitat loss and degradation threatens the survival of orchids on Madagascar, including *M. regalis* (IUCN Orchid Specialist Group 1996). **(RN)**

Uses

None recorded. **(PC)**

Cultivation

Compost C. **(CB)**

Taxonomic notes

The most recent account of the genus is given by Perrier de la Bâthie (1939). An updated nomenclature is provided by Du Puy *et al.* (1999). **(PC)**

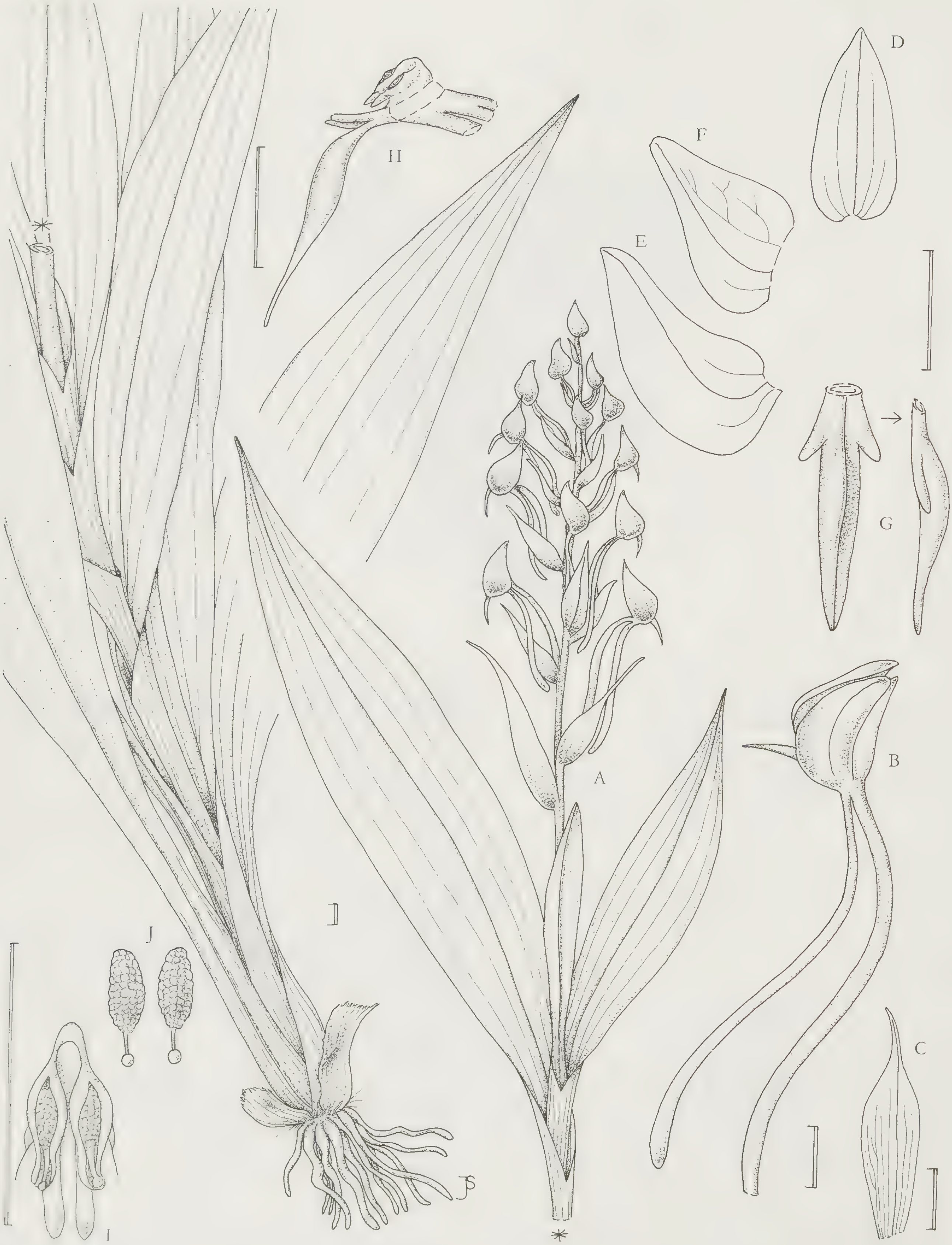

Fig. 83.1. *Megalorchis regalis* (Schltr.) H. Perrier. A. Habit; B. Flower; C. Bract; D. Dorsal sepal; E. Lateral sepal; F. Petal; G. Labellum; H. Labellum and column, side view; I. Column, front view; J. Pollinaria. Double bar = 1 cm. Drawn by Judi Stone from *Perrier 15263* (P).

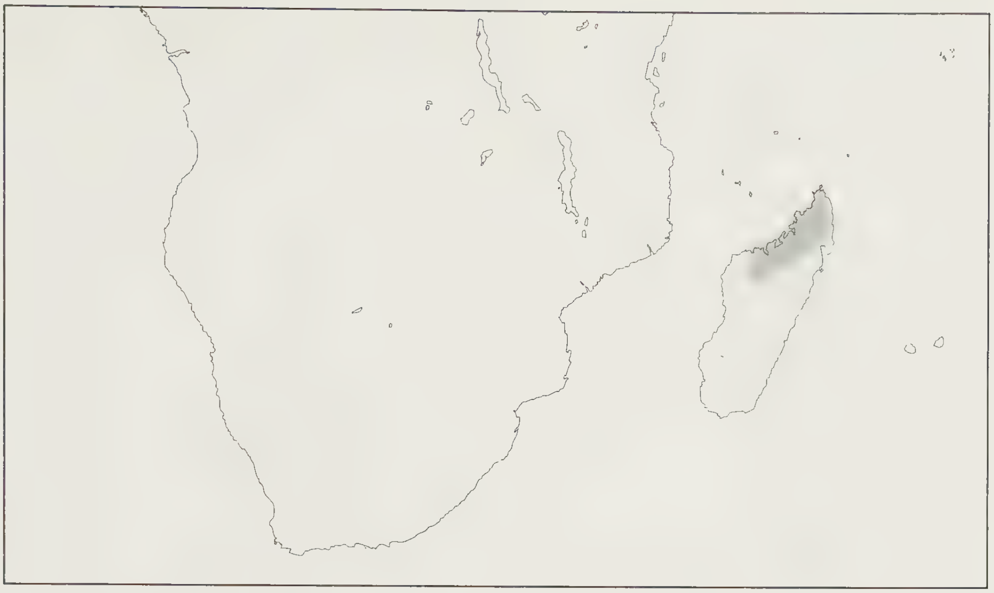

Fig. 83.2. Distribution map of *Megalorchis.*

Taxonomic literature

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84. NEOBOLUSIA

Neobolusia Schltr., *Bot. Jahrb. Syst.*, **20**, *Beibl.*, **50**, 5 (1895). Type species: *Neobolusia tysonii* (Bolus) Schltr.

Brachycorythis sensu Rolfe, *Fl. Cap.*, **5**, 3, 84 (1912), pro parte.

Derivation of name

From the Greek *neos*, new, and Harry Bolus (1834–1911), the eminent South African orchidologist, founder of the Bolus Herbarium at the University of Cape Town. **(HK, PL)**

Description (Plate 103; Fig. 84.1)

Slender terrestrial *herbs* with testicular tubers and a few unbranched roots. *Stem* to 50 cm tall, glabrous, green, erect. *Leaves* basal and cauline, elliptic to oblong, acute, glabrous; basal leaves one to three, spreading; cauline leaves smaller, sheathing, grading above into floral bracts. *Inflorescence* terminal, lax; bracts as large as ovaries to one-third larger, ovate-lanceolate. *Flowers* comparatively few, resupinate, with green sepals and white to pink petals and lip. *Dorsal sepal* narrowly elliptic, acute, slightly hooded. *Lateral sepals* similar in shape, spreading. *Petals* broadly oblique, obtuse, cohering with and nearly as long as sepals, basally fused to column. *Labellum* simple or three-lobed, ovate, unspurred, weakly differentiated into shallowly concave hypochile and flat epichile, with a callus in the lower part. *Column* erect, slender; anther thecae erect, parallel and adjacent; auricles small; pollinia sectile, with a short caudicles and two large naked viscidia; stigma cushion-like, in a cavity below the rostellum, tripulvinate with the mid-lobe the smallest; rostellum three-lobed with small central lobe, lateral lobes large. *Capsule* oblong. **(HK, PL)**

Distribution (Fig. 84.2)

Neobolusia comprises three species in the summer-rainfall region in southern and south-central Africa. **(HK, PL)**

Ecology

Members of the African genus *Neobolusia* are terrestrial herbs that grow in montane and alpine grassland, often in damp areas among rocks on seepage slopes or along stream banks. They occur at high elevations. *Neobolusia ciliata* Summerh. has been recorded from the Chimanimani Mountains in Zimbabwe and Mozambique at 1540–2000 m and *N. stolzii* from the Nyika Plateau in Zambia at 2150 m (Schelpe 1966; la Croix and Cribb 1995). Within the range of the genus, the distribution of individual species can be widespread, as with *N. tysonii*, which extends from the eastern Cape Province, through the higher parts of the Natal and the eastern Orange Free State to the eastern Transvaal, although its occurrence is said to be sporadic (Schelpe 1966).

Neobolusia usually flowers between December and March, the slender stems with a basal rosette of leaves, arising from the small ovoid, ellipsoid or fusiform tubers underground. Some evidence of the occurrence of fruit-set in the genus is provided by a specimen collected from the Chimanimani Mountains in Zimbabawe on 31 January 1954, on which both flowers and fruits were found (la Croix and Cribb 1995). **(RN)**

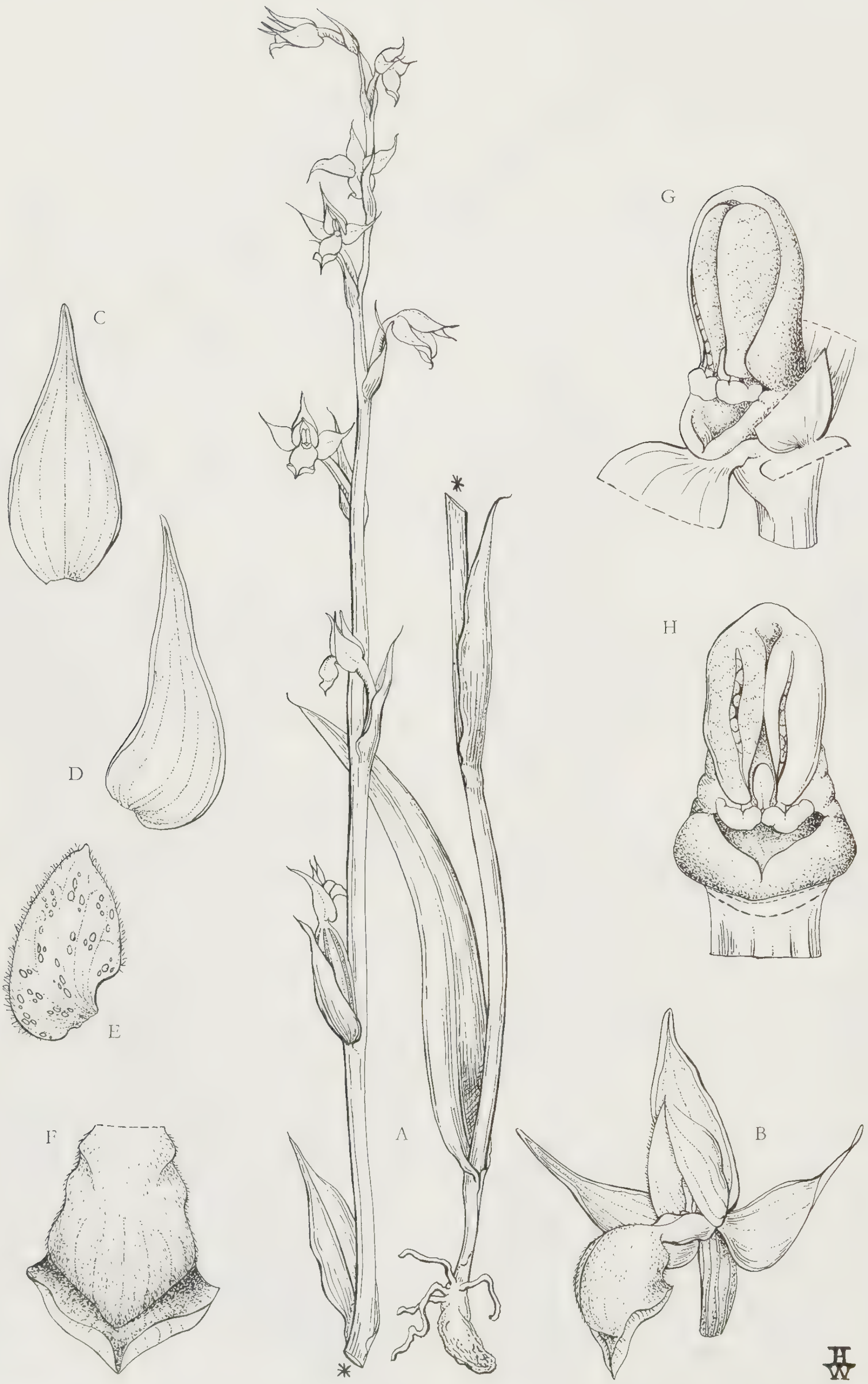

Fig. 84.1. *Neobolusia stolzii* Schltr. A. Habit, ×1; B. Flower, oblique view, ×3; C. Dorsal sepal, ×4; D. Lateral sepal, ×4; E. Petal, ×4; F. Labellum, ×4; G. Column, side view, sepals and petals removed, ×15; H. Column, front view, ×15. Drawn by Heather Wood from *Stolz 1076* and *Ball 800.*

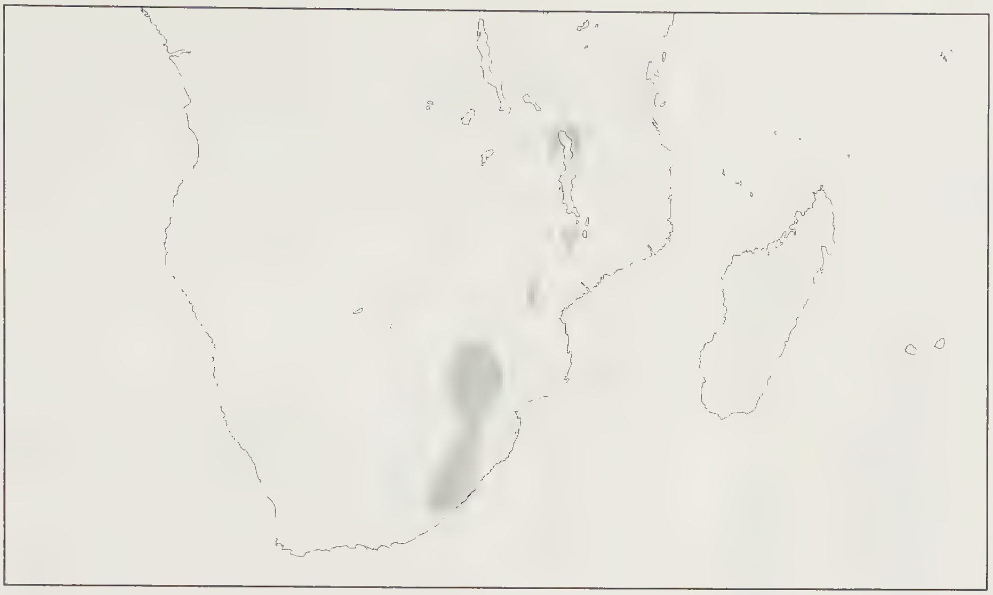

Fig. 84.2. Distribution map of *Neobolusia.*

Phylogenetics

The genus is usually considered closely related to *Brachycorythis* (Bolus 1893, 1894, 1895, 1896; Schlechter 1926; Senghas 1973, 1974), as suggested by a similar flower structure: spreading and equally long sepals and petals, spreading lip which is ± concave in its basal part, unstalked column with erect or suberect anther and small auricles, pad- or cushion-like stigma, and three-lobed rostellum. Dressler (1981) noted that *Brachycorythis* is 'suggestive of a general sort of Orchidinae', thereby apparently implying that the genus is close to the ancestral form in the subtribe. The only distinguishing feature between *Neobolusia* and *Brachycorythis* is the shallowly concave lip of *Neobolusia*, which has a callus in the lower portion. *Brachycorythis*, on the other hand, has a deeply saccate or spurred lip and lacks the callus. For this reason *Neobolusia* is maintained as a separate genus in the recent taxonomic literature (e.g. Dressler 1981, 1993). However, several lines of development can be identified in *Brachycorythis*, both in morphological features and ecological adaptations, and it has been suggested that *Neobolusia* is another line of development within *Brachycorythis* that has evolved in adaptation to montane grasslands (Kurzweil and Weber 1991).

A lip with a prominent spur has been interpreted as the primitive condition (Summerhayes 1955), and its evolution into a saccate lip hypochile would then be derived. *Neobolusia* seems to be the final stage of the reduction of the spur that can be observed in *Brachycorythis* (Kurzweil and Weber 1991). A deeply three-lobed lip is apparently primitive in *Brachycorythis*, and a gradual reduction of the lobing is apparent in the genus (Summerhayes 1955). The lip is unlobed in two species of *Neobolusia*, and the three-lobed lip of *N. ciliata* is probably an ancestral feature. **(HK, PL)**

Uses

None recorded. **(HK, PL)**

Cultivation

Neobolusia plants may be grown in compost C or D. **(CB)**

Taxonomic literature

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85. NEOTINEA

Neotinea Rchb.f., *Poll. Orch. Gen.*, 29 (1852). Type species: *Neotinea maculata* (Desf.) Stearn.

Tinea Biv., *Gior. di scienz. lett. arti per la Sicilia*, 149 (1833). Type species: *Tinea cylindrica* Biv. (=*Neotinea maculata* (Desf.) Stearn).

Tinaea Vis., *Fl. Dalmat.*, **3**, 354 (1852), sphalm. pro *Tinea* Biv.

Derivation of name

From the Greek *neos*, new, and Vincenzo Tineo (1791–1856), a Sicilian botanist. **(JW)**

Description (Plates 104, 105; Fig. 85.1)

Small *herbs*. *Rootstock* tuberous, tubers two, entire, globose or ellipsoid. *Stem* often rather glaucous, erect. *Leaves* 2–4 basal, 1–2 cauline, spotted or unspotted. *Inflorescence* cylindrical, sometimes conical, dense, sometimes slightly twisted; floral bracts thin, membranous. *Flowers* small, greenish white, straw-coloured, whitish or pink, often spotted and lined darker pink or purple. *Sepals* and *petals* connivent, forming a hood. *Labellum* three-lobed, mid-lobe often bilobed, spurred, without calli, often minutely papillose, spur short and conical, or longer and cylindrical. *Column* short, with two large lateral stigmas joined below; anther prominent; pollinia two, each with a short caudicle attached to a viscidium enclosed in a single simple bursicle. *Ovary* cylindrical to fusiform, sessile, twisted, glabrous. **(JW)**

Distribution (Fig. 85.2)

Four species distributed from western Ireland and the Isle of Man eastward across southern Europe from Portugal and the Canary Islands to Turkey and the Lebanon, south to North Africa, east to the Caucasus, Iraq, and the Caspian region in western Asia. **(JW)**

Palynology

Sculpturing of *N. intacta* (Link) Rchb.f. (= *N. maculata*) is ± hamulate, whereas that of *N. tridentata* (cited as *Orchis tridentata*) and *N. ustulata* (cited as *Orchis ustulata*) is laevigate-scabrate (Schill and Pfeiffer 1977). **(AP)**

Cytogenetics

Cytological studies in *Neotinea* revealed a chromosome number of $2n = 2x = 42$. The only exception is *Neotinea tridentata* subsp. *commutata* with $2n = 4x = 84$ (Mazzola *et al.* 1981). Observations of $2n = 42 + 1B$ have also been made for *Neotinea tridentata* subsp. *tridentata* and *N. ustulata* (D'Emerico *et al.* 1990, 1992). These chromosome numbers have been reported for some individuals found in stations at the boundary of their distribution area, and that may be correlated with B-chromosome presence (D'Emerico *et al.* 1993).

Comparative studies of karyotypes in *Anacamptis* ($2n = 32, 36$) and *Neotinea* ($2n = 42$) show that the karyotype morphology of the latter differs in having smaller chromosomes and a more complex karyomorphology (Fig. C.2e). Consequently, only in *N. tridentata* subsp. *tridentata* and *N. lactea* has it been possible to construct the karyotype. The karyotype of these species consists mainly of metacentric chromosomes. However, the karyotype of *N. lactea* is more asymmetrical than that of *N. tridentata* subsp. *tridentata* (D'Emerico *et al.* 1990, 1992). Giemsa C-banding in *N. lactea* revealed large telomeric bands in addition to centromeric bands. However, in this species the complex karyotype morphology made it difficult to study the banding pattern. **(SD)**

Phytochemistry

The phenolic glucoside loroglossin was isolated from *N. ustulata* (cited as *Orchis ustulata*; Delauney 1925*a*, *b*) and its structure later determined to be *bis*[4-(β-D-glucopyranosyloxy)benzyl] *erythroiso*-butyltartrate by Aasen *et al.* (1975; Fig. 81.4).

Investigation of the flavonoid content of leaves of *N. ustulata* revealed the presence of quercetin. This flavonol aglycone was detected in acid-hydrolysed extracts of leaf tissue, indicating that it originates from quercetin *O*-glycosides (C. A. Williams 1979). An examination of the anthocyanin content of *N. ustulata* flowers indicated that they contain cyanidin 3-glucoside (chrysanthemin) and cyanidin 3-diglucoside (mecocyanin) in the ratio 1:9 respectively. The minor anthocyanin, cyanidin 3-glucoside, was found only in flower buds and at the beginning of the anthesis (Uphoff 1979).

Baytop and Sezik (1968) reported on the chemical analysis of tubers of *Orchis* species collected in south-west Anatolia, Turkey. Their results were summarized in a later review by Ernst and Rodriguez (1984). The *Neotinea* species analysed was *N. tridentata* (cited as *Orchis tridentata*). See *Anacamptis*. **(NV, RG)**

Ecology

Neotinea normally grows on alkaline soils (Davies *et al.* 1988; Delforge 1995). *Neotinea maculata* has principally been recorded from limestone areas, such as the west of Ireland and from calcareous sea sand, such as the stabilized sand-dunes on the Isle of Man (Lang 1989). In Britain, *N. ustulata* most frequently occurs in the chalk districts of southern England (Lang 1989). Farther north in England it has also been recorded from the Carboniferous limestone areas of Derbyshire, Yorkshire, Cumbria, northern Lincolnshire, and eastern Yorkshire (Foley 1987). In all of these cases the soils are relatively warm and dry (Summerhayes 1985), although in some parts of its European range, *N. ustulata* at least can grow in wetter soils (Delforge 1995). Some members of the genus can also grow in more acidic conditions. In a few sites in Ireland *N. maculata* occurs on semi-peaty soils overlying acid soils, and in the French and Italian Riviera it grows in soils formed from non-calcareous rocks (Summerhayes 1985). The pH range of soils in which *N. ustulata* occurs has also been reported as ranging from 5.2–7.3 (Arditti 1992), although relatively high calcium levels have been recorded in another study for soils in which *N. ustulata* and *N. tridentata* naturally grow (concentrations of 534.3 mg and 426 mg/100 g soil, respectively; Möller 1985, cited in Arditti 1992).

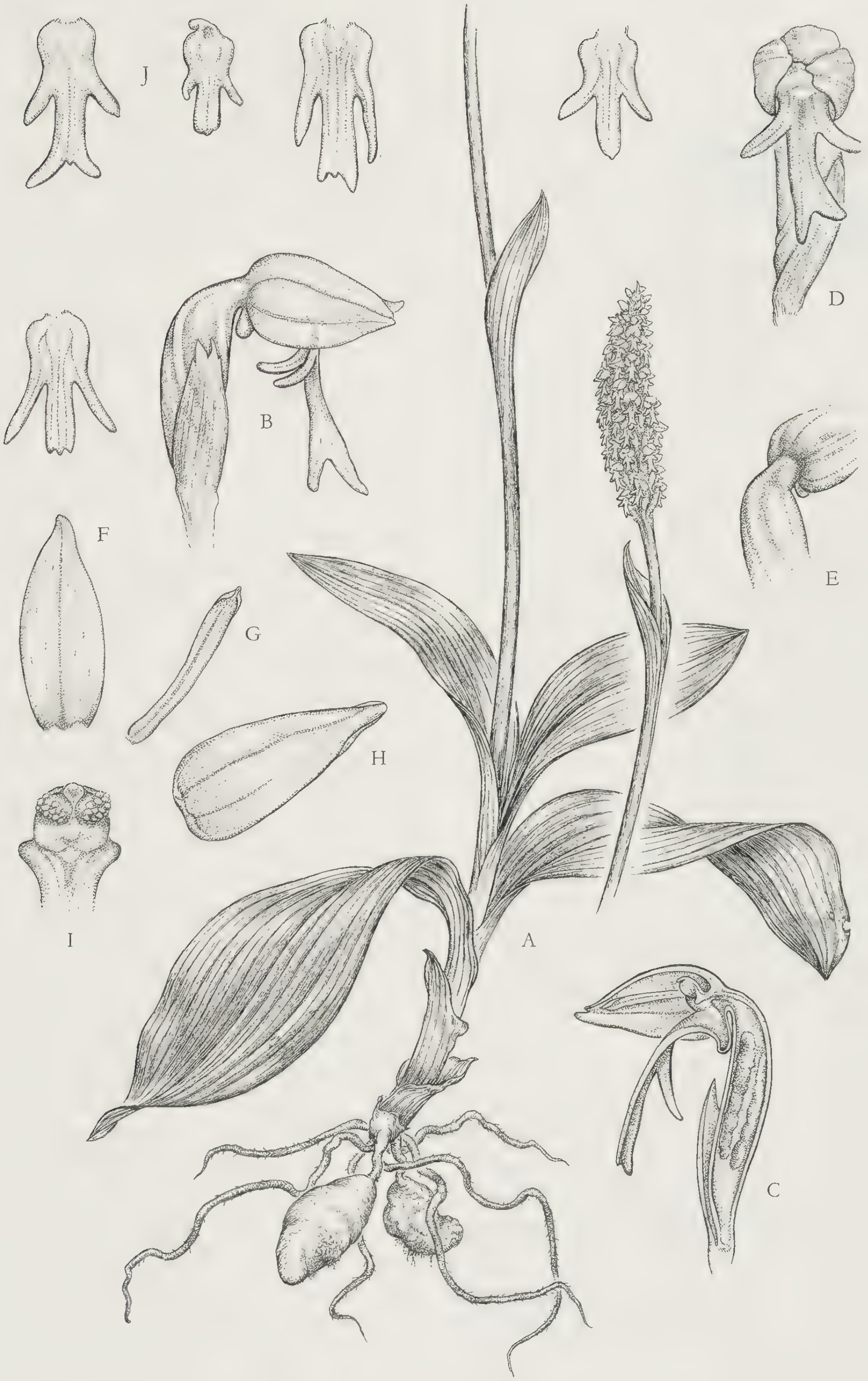

Fig. 85.1. *Neotinea maculata* (Desf.) Stearn. A. Habit and inflorescence, ×1; B. Flower and bract from side, ×6; C. Flower and bract, longitudinal section, ×6; D. Flower and ovary from front, ×6; E. Apex of ovary/base of perianth, ×6; F. Dorsal sepal, ×9; G. Petal, ×9; H. Lateral sepal, ×9; I. Column apex and anther, ×9; J. Labellum variation, ×6. Drawn by Oliver Q. Whalley from Kew Spirit Collection nos. 43651, 43717, 25873, and 43551.

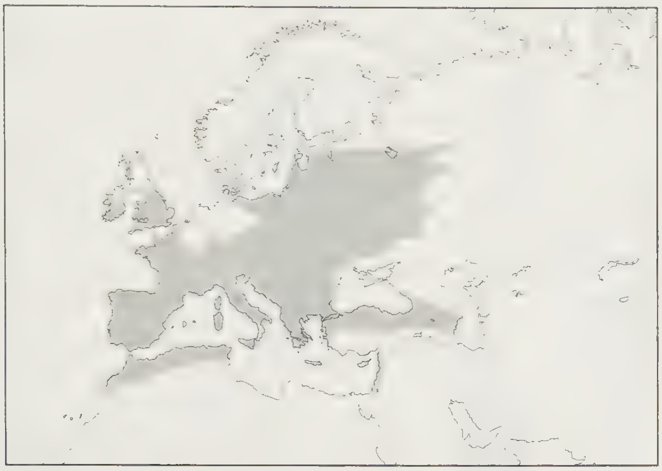

Fig. 85.2. Distribution map of *Neotinea.*

Neotinea can grow under conditions of full sun to shade in a range of habitats encompassing grassland, scrubland (including garrigue and maquis) and woodlands, and at both high and low elevations (Delforge 1995). In Cyprus, for example, *N. maculata* occurs in two distinct types of habitats: in pine forests high in the mountains, which comprise the southern part of the Troodos range, and on bare chalk soils on low ground near the sea (Davies *et al.* 1988). At lower-elevation locations on the island the two colour forms (pink and white flowers) of the species are found growing together, whereas in the mountains only the white form occurs. Similarly in the west of Ireland, *N. maculata* has long been associated with the limestone pavement, grassy pastures, and roadside verges of the Burren (Summerhayes 1951), but in recent years it has also been found growing in scrubby mixed ash and hazel woodland (Doyle 1985; Lang 1989). These woodland plants resemble more closely those of Mediterranean colonies in that their inflorescences are more robust and taller than those of the more open habitats in the Burren (Lang 1989).

Elsewhere in the British Isles, *N. maculata* occurs at low elevations on stabilized sand-dunes (Lang 1989), whereas in parts of its range in mainland Europe it can occur in mountain locations at up to 2000 m (Delforge 1995). Other members of the genus are also reported from high elevations. *Neotinea lactea* occurs up to 1800 m in some localities and is said to be particularly frequent in mountain pastures on limestone. *Neotinea tridentata* occurs in alpine meadows, grassy hillsides, and open woodland at up to 1600 m (Davies *et al.* 1988; Delforge 1995). Similarly, *N. ustulata* is often found in mountainous areas and can occur at elevations of up to 2400 m in alpine pastures. It is perhaps less tolerant of shade than congeneric species, being rarely found in garrigue or open woodland. In the British Isles it is usually found among the grasses of well-drained chalk downland in sheltered, sunny situations that are often south-facing, although it does sometimes occur in areas of juniper scrub where it may co-occur with *Anacamptis morio* (Lang 1989).

Flowering of *Neotinea* takes place sometime between early spring and late summer depending on the species and the location of its populations. The earliest flowering member of the genus is *N. lactea*, which blooms in February in North Africa (Davies *et al.* 1988) and reaches anthesis by April or May in other parts of it range. *Neotinea maculata* also flowers early, between mid-March and May (Davies *et al.* 1988). Summerhayes (1951) attributed its early flowering in the Burren to its 'winter-green' habit whereby the aerial shoots have already developed in the autumn preceding emergence of the inflorescence. Peak flowering is normally in May, which is before that of co-occuring orchids such as *Spiranthes spiralis*, *Ophrys apifera*, *Anacamptis pyramidalis*, and *Epipactis atrorubens* (Hoffman ex Bernh.) Besser. The flowering period of individual plants is relatively short and, as with the Isle of Man populations, Lang (1989) suggested senescence may be accelerated by seasonal high winds in these exposed areas, although it may simply be the result of rapid fruit-set as seems to be the case with *N. ustulata*. *Neotinea maculata* completes anthesis and capsule formation within about one month in southern England (Lang 1989). *Neotinea tridentata* and *N. ustulata* flower relatively late, between April and August throughout their ranges (Davies *et al.* 1988; Delforge 1995). In Britain, most plants of *N. ustulata* flower in May–June in the south of England and a little later farther north (Summerhayes 1951). However, a form has been discovered recently at five sites in East Sussex and Hampshire on the south coast of England that flowers in July (Lang 1989). Individual plants can flower for at least two consecutive years (Lang 1989), but flowering of populations is highly variable and influenced by rainfall levels (Foley 1987; Lang 1989) such that in drought years no flowering may occur at all (Lang 1989). Not all populations of *N. ustulata* are winter-green, however, because some retain their leaves throughout the summer. Rasmussen (1995) suggested that this indicates the occurrence of different ecological races within this species.

Fruit-set in this genus is expected to be low because its members are nectarless (cf. Neiland and Wilcock 1998). An observation of 11.8% of flowers setting fruit among a population of *N. ustulata* on Öland, Sweden, in the summer of 1998 conforms to this expectation (Neiland and Wilcock, personal observation). An exception may be *N. maculata*, which casual observations indicate may have much higher levels of fruit and seed production. Also, *N. maculata* is said to be self-pollinating (Summerhayes 1951; Davies *et al.* 1988; Lang 1989) and may even be cleistogamous (Delforge 1995). Once seed germination has taken place, *Neotinea* plants remain underground as a protocorm/mycorrhizome until the first root and aerial shoot develops, followed by formation of a tuber (Rasmussen 1995). Progression to the aerial stage is believed to occur rapidly in *N. tridentata*, which has been observed to produce its first leaf above ground in its second growing season (Beer 1863, cited in Rasmussen 1995). In contrast, *N. ustulata* is frequently quoted as having a long initial life underground of 10–15 years as a protocorm during which time it is entirely dependent on mycorrhizal nutrition (Stonjanow 1916; Zuchs and Ziegenspeck 1927, cited in Rasmusssen 1995; Summerhayes 1951; Wells 1981; Davies *et al.* 1988). The protocorm may be as long as

20–30 mm before roots and leaves are formed and have many constrictions along its length, which are taken to indicate each year's growth. However, Rasmussen (1995) suggested that their use may lead to inaccurate age estimates because constriction lines can also arise from contraction of the protocorm or from nodes. She stated that cultivated seedlings of *N. ustulata* are rarely constricted and cited work by Möller (1985) in which cultivated *N. ustulata* plants reached the flowering stage within three years as evidence, casting doubt on the accuracy of the long-age estimates of *N. ustulata* seedling stages.

Neotinea is rare throughout many parts of its distribution. For example, *N. tridentata* is said to be quite rare in the western limits of its range, although it is relatively common in Anatolia, Turkey (Delforge 1995). *Netinea ustulata* is described as local and unpredictable in its appearance, although it may sometimes be abundant, especially in mountain areas (Summerhayes 1951; Delforge 1995). Recently new records in western Ireland of *N. maculata* have extended the range of this species beyond the Burren in County Clare where it was first discovered by F. M. Moore in 1864. It is now known to occur from west Donegal southward to east Cork (Shepherd and Shepherd 1985; Lang 1989), but it remains a rare orchid in Ireland as elsewhere in Europe (Delforge 1995). Its western and coastal locations indicate that it is adapted to a relatively warm oceanic climate (Summerhayes 1951), and its unusual disjunct distribution in the British Isles and Mediterranean is explained by fluctuations in climatic conditions in the past. The Irish populations of *N. maculata* are thought to be preglacial or inter-glacial relicts from a period of much warmer climatic conditions when this species and other Mediterranean plants still growing in the Burren would have been able to migrate northward across a continuous land bridge from the present-day Iberian peninsula. The ameliorating conditions of the Atlantic Ocean on the local climate during and after the Ice Age are thought to have allowed such species to persist in the west of Ireland when they were unable to do so in the rest of the glaciated British Isles (Summerhayes 1951). By comparison, the other isolated populations of *N. maculata* in the British Isles discovered on the Isle of Man in 1969 are probably of much more recent origin. Because of their visual resemblance to the plants from the Burren (white flowers and unspotted leaves), they are thought to have spread from western Ireland to Britain via seeds dispersed either by the wind or sea currents (Lang 1989).

The British distribution of another rare member of the genus, *N. ustulata*, has shown a marked decline in recent years due to habitat loss and agricultural practices. For example, in a survey of northern English populations, Foley (1987) found that from 118 previously recorded sites of the species, only 15 colonies still survived. The largest of these comprised over 200 plants, but the majority comprised 35 or fewer individuals. He estimated that there were probably less than 500 flowering plants still surviving in the whole of the north of England distribution area at the time of the survey. In the southern counties of England, *N. ustulata* can still be found flowering in large numbers at some suitable sites on the chalk downland (Lang 1989) but has also disappeared from some previous known localities. In Suffolk, for example, it is estimated that it had gone from the county by 1840 (Sanford 1991). The number and extent of *N. ustulata* populations elsewhere in its European range is also declining, for example in southern Scandinavia (Petterson 1976) where it is being lost from grassland. The principal explanation for the reduction in Britain and other countries seems to be agricultural improvement of ancient pastures through the application of inorganic fertilizers and disturbance by ploughing (Foley 1987). Map records show that ploughing of prime field sites in Suffolk in the 19th century resulted in rapid loss of this species from the area (Sanford 1991), and in Derbyshire the species survives only in upland pastures, which are difficult to upgrade for agricultural purposes (Foley 1987). Absence of grazing may also lead to competition by aggressive grass species, which rapidly out-compete this orchid. **(RN)**

Pollination

The small flowers of *N. maculata* contain nectar. However, no insect pollinators have been reported in the literature (van der Cingel 1995). The fact that seed set is generally high and that self-pollination occurs readily indicate that *N. maculata* is exclusively self-pollinated. All other members of the genus *Neotinea* are nectarless and pollinated by deceit. Vöth (1984) found that the tachinid fly *Echinomyia magnicornis* is the regular pollinator of *N. ustulata*. Its floral morphology allows the flies to access the spur entrance while sitting above the flower, not on the labellum. Other insects that may be involved in the pollination of *N. ustulata* are beetles and bees (van der Cingel 1995). The relatively late-flowering of *N. tridentata* is considered an adaptation to the period of brood care of the solitary bee *Osmia bicolor*, which visits and pollinates this species. However, a large number of other flower visitors, which may at least occasionally carry pollinaria, have been reported (Reinhard *et al.* 1991; Vöth 1992). **(AW, SC, AD)**

Uses

None recorded. **(JW)**

Cultivation

Species of *Neotinea* grow on slightly acid to alkaline soils and can be successfully grow in compost C. **(CB)**

Taxonomic literature

Bateman, R. M., Pridgeon, A. M., and Chase, M. W. (1997). Phylogenetics of subtribe Orchidinae (Orchidoideae, Orchidaceae) based on nuclear ITS sequences. 2. Infrageneric relationships and reclassification to achieve monophyly of *Orchis sensu stricto*. *Lindleyana*, **12**, 113–41.

Delforge, P. (1995). *Orchids of Britain and Europe*. HarperCollins, London.

Stearn, W. T. (1975). *Multum pro parvo*: the nomenclatural history and synonymy of *Neotinea maculata* (Orchidaceae). *Annals of th Goulandris Museum*, **2**, 69–81.

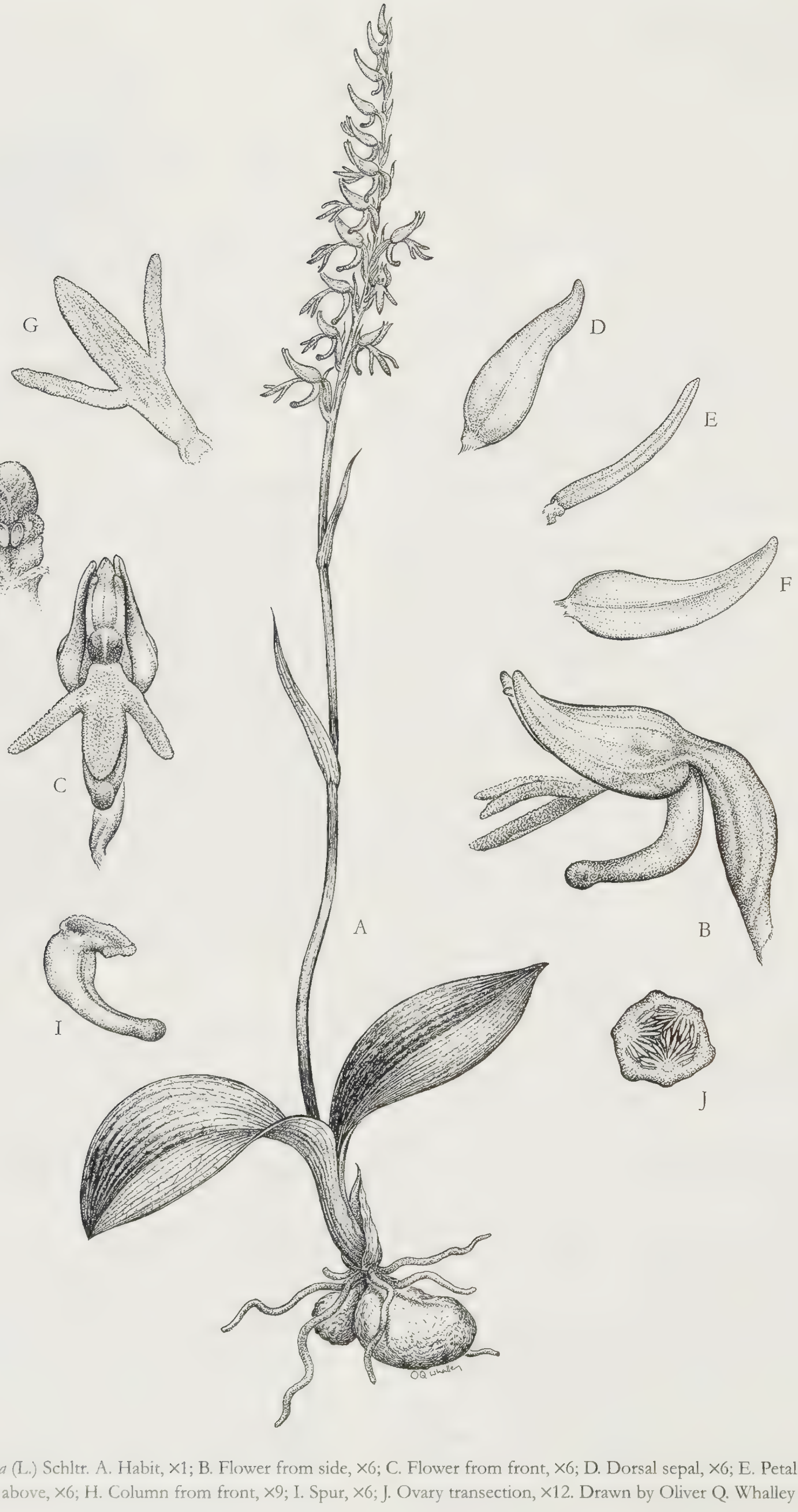

Fig. 86.1. *Neottianthe cucullata* (L.) Schltr. A. Habit, ×1; B. Flower from side, ×6; C. Flower from front, ×6; D. Dorsal sepal, ×6; E. Petal, ×6; F. Lateral sepal, ×6; G. Labellum from above, ×6; H. Column from front, ×9; I. Spur, ×6; J. Ovary transection, ×12. Drawn by Oliver Q. Whalley from Kew Spirit Collection no. 50469.

86. NEOTTIANTHE

Neottianthe Schltr., *Feddes Repert.*, **16**, 290 (1919). Type species: *Neottianthe cucullata* (L.) Schltr.

Derivation of name

From the Greek *Neottia*, a genus of orchids, and *anthos*, flower, alluding to the superficial resemblance of the flowers to some Asiatic species of *Neottia*. **(JW)**

Description (Plate 106; Fig. 86.1)

Slender *herbs*. *Rootstock* tuberous, tubers two, oblong or ellipsoid, often somewhat concave. *Stem* with several sheathing bracts. *Leaves* two, basal, unspotted. *Inflorescence* few- to many-flowered, rarely with a solitary flower, lax, often secund; floral bracts herbaceous. *Flowers* resupinate, pink or purple. *Sepals* and *petals* connivent, forming a hood. *Labellum* spurred, three-lobed, usually papillose above, spur often incurved, conical. *Column* suberect, rostellum three-lobed; pollinia two, with very short caudicles; viscidia placed close together and parallel above the stigma; bursicles absent. *Ovary* subsessile, cylindrical to fusiform, gently twisted, glabrous. **(JW)**

Distribution (Fig. 86.2)

Approximately 11 species distributed in north-east Europe and temperate Asia from the Baltic states east to China, Japan, and the Himalayan region. **(JW)**

Palynology

Sculpturing of *N. cucullata* is laevigate-perforate (Schill and Pfeiffer 1977). **(AP)**

Ecology

Neottianthe plants grow in the deep, damp, acid soils of prime coniferous forests, especially in damp, mossy places, where it is in semi-shade or shade. Less often it grows in mixed woods or oak woods and normally at elevations of not more than 500 m. Occasionally it

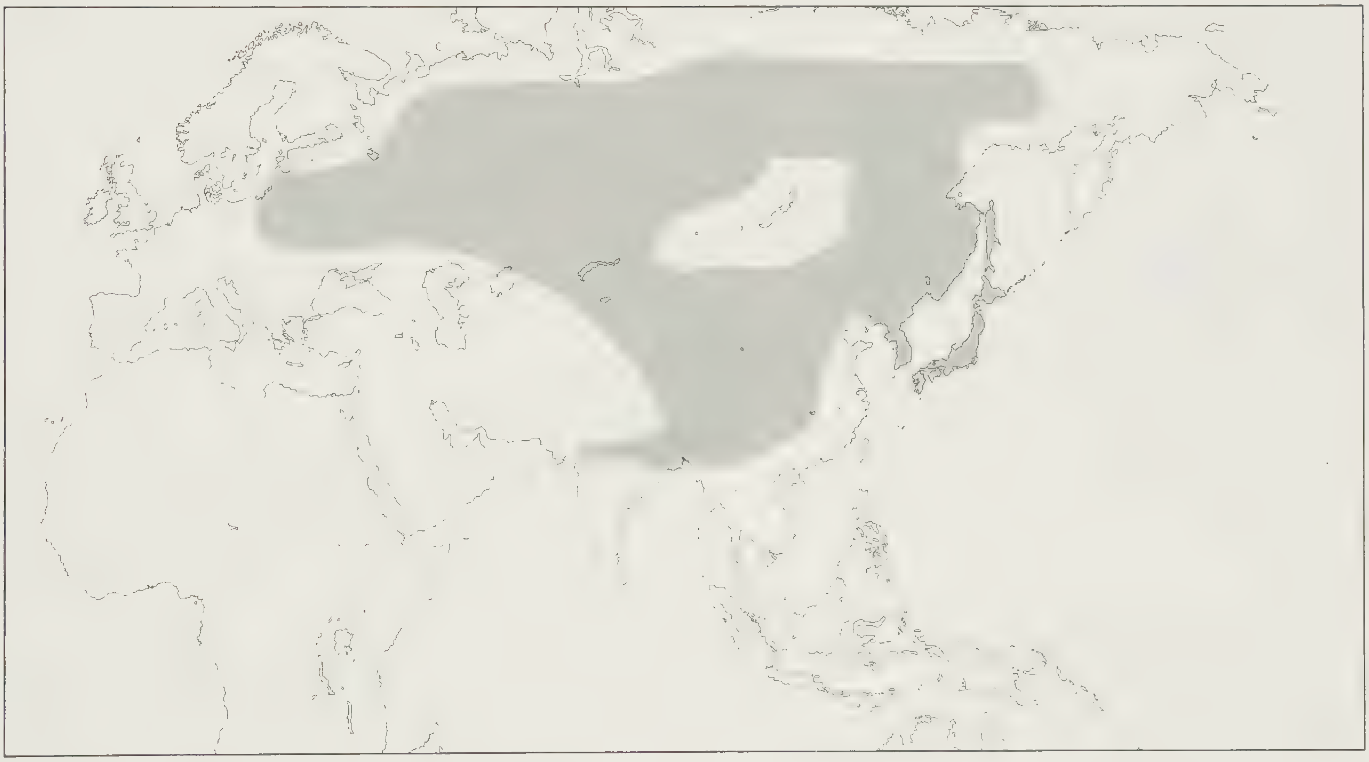

Fig. 86.2. Distribution map of *Neottianthe*.

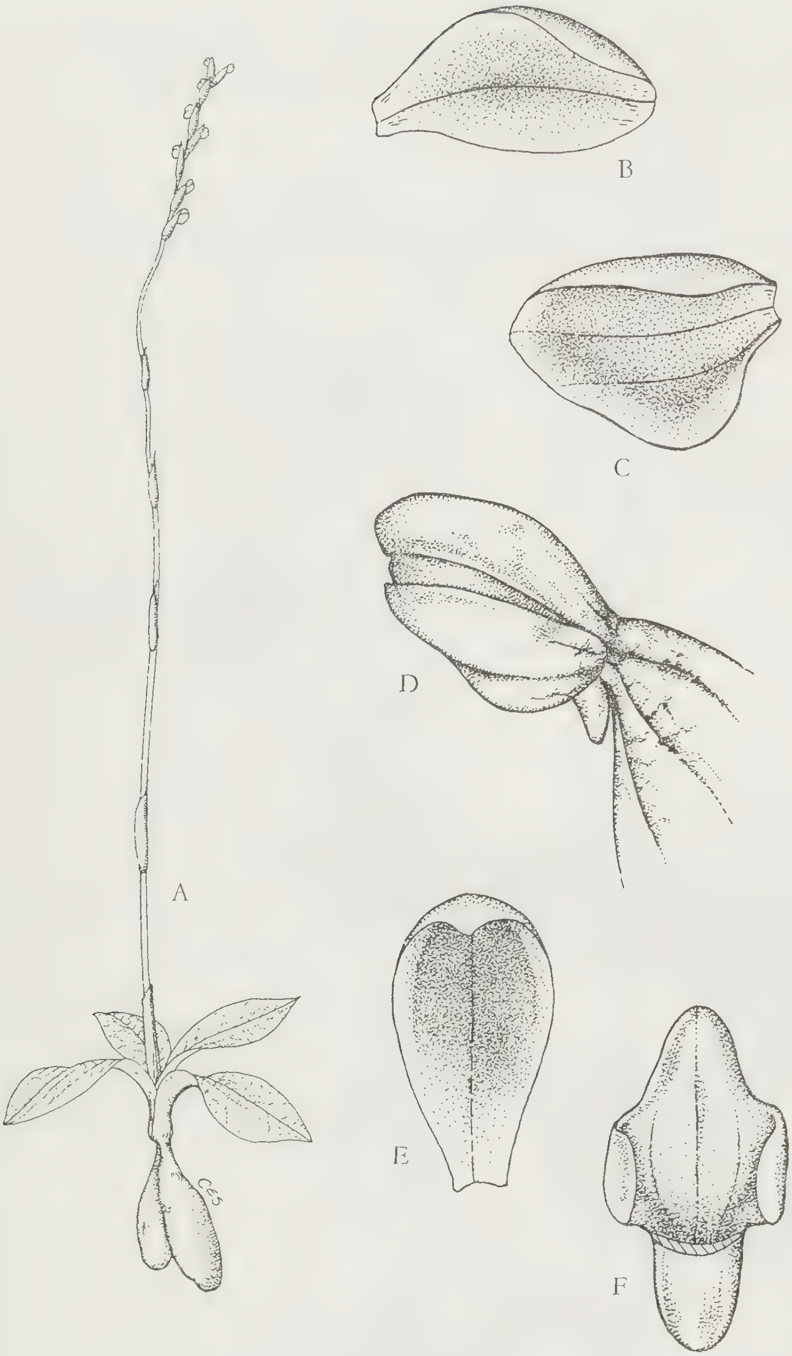

Fig. 87.1. *Oligophyton drummondii* H. P. Linder & G. Will. A. Habit, ×1; B. Lateral sepal, ×20; C. Petal, ×20; D. Flower, side view, ×15; E. Dorsal sepal, ×20; F. Labellum, ×20. Drawn by Clair Smith from *Ball 952*.

occurs in mountain meadows and has been recorded from alkaline marshes in Japan at up to 2000 m (Rawat and Pangtey 1985; Davies *et al.* 1988; Delforge 1995).

Flowering of *Neottianthe cucullata* is most often seen in July and August but can occur from May to October in different parts of the range. It perennates by means of ovoid tubers and has two basal leaves. It often flowers at the same time as another orchid of coniferous woodlands, *Goodyera repens* (L.) R.Br. It is regarded as local and rare throughout its distribution. **(RN)**

Uses

In China *Neottianthe* plants are collected for use in herbal medicine to improve blood circulation (Chen and Tang 1982). **(RN)**

Cultivation

Species of *Neottianthe* occur in mountains in conifer forests and alpine meadows. They should be grown in compost C or D. **(CB)**

87. OLIGOPHYTON

Oligophyton H. P. Linder, *Kew Bull.*, **41** (2), 314 (1986). Type species: *O. drummondii* H. P. Linder

Derivation of name

From the Greek *oligos*, few or short, and *phyton*, a plant, referring to the stature of the plant. **(PC)**

Description (Fig. 87.1)

Terrestrial *herbs* perennating by testicular tubers. *Leaves* dimorphic, with ovate, spreading, basal leaves and loosely convoluted cauline leaves. *Inflorescence* an erect lax spike; bracts half as long as the ovaries, green to somewhat chartaceous. *Flowers* small, more or less resupinate, with the sepals and petals not spreading. *Sepals* free, entire, one-nerved. *Petals* more or less enclosed by the sepals, three-nerved, slightly shorter than the sepals. *Labellum* shorter than the sepals and petals and enclosed by them, three-lobed and three-nerved, the side lobes blunt and shorter than the mid-lobe; spur short, straight or curved. *Column* short; rostellum square with a small mid-lobe; viscidia separate and held in shallow notches in the rostellum side lobes; lateral appendages minute; anther erect, two-celled; stigma two-lobed, the lobes sessile, slightly convex, diverging from the base. *Ovary* twisted. **(PC)**

Distribution (Fig. 87.2)

A monospecific genus endemic to eastern Zimbabwe. **(PC)**

Ecology

The Zimbabwean endemic *O. drummondii* is found in the montane zone of the Chimanimani mountain area, growing in sandy, quartzitic soil. It is a terrestrial herb that perennates by means of tubers and flowers in September and October (la Croix and Cribb 1995). **(RN)**

Uses

None recorded. **(PC)**

Cultivation

Compost C or E. **(CB)**

Taxonomic notes

The taxonomic affinites of this monospecific genus are thought to lie with *Habenaria* and *Benthamia*, the latter a Madagascan genus. *Oligophyton* has only been collected three times; more material is needed to assess its affinities. **(PC)**

88. OPHRYS

Ophrys L., *Sp. Plant.*, ed. 1, 945 (1753). Type species: *Ophrys insectifera* L.

Derivation of name

From the Greek *ophrys*, eyebrow, a name for a plant of uncertain identity (perhaps *Listera ovata* (L.) R.Br.) used by Pliny, who mentions its use to blacken eyebrows or hair; the name equally could be an allusion to the resemblance of the curved sepals of some species to an arched eyebrow. **(JW)**

Description (Plate 107; Fig. 88.1)

Mostly small perennial *herbs. Rootstock* tuberous, tubers two (sometimes three), globose or ovoid, entire, sessile or stipitate. *Stem* glabrous. *Leaves* basal, rosulate and/or cauline, unspotted. *Inflorescence* lax. *Flowers* usually showy, insectiform. *Sepals* and *petals* free, ± spreading. Sepals larger, sometimes reflexed, usually glabrous, green, rose-pink, or whitish. Petals smaller, glabrous or hirsute. *Labellum* spurless, flattened, arcuate or strongly convex, entire, subentire or three-lobed, sometimes with two conical lateral protuberances at the base, or at the base of the lateral lobes, often with a distinct, deflexed, horizontal or upturned, glabrous apical appendage (which sometimes has a hair tuft at its base) or a less distinct apical mucro, velutinous above, with a variously shaped, often shiny, glabrous central area or markings (speculum), above which, in

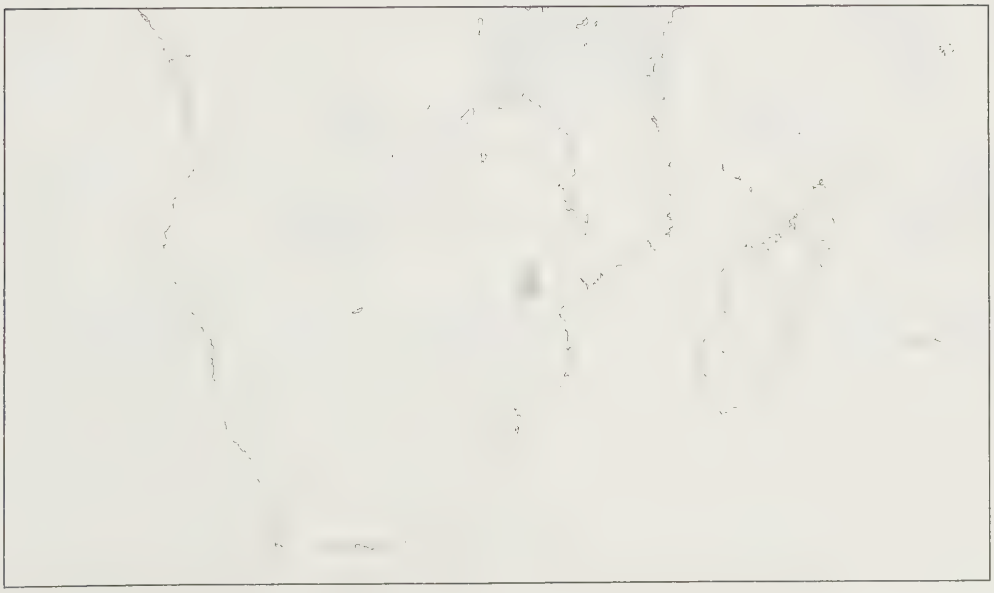

Fig. 87.2. Distribution map of *Oligophyton.*

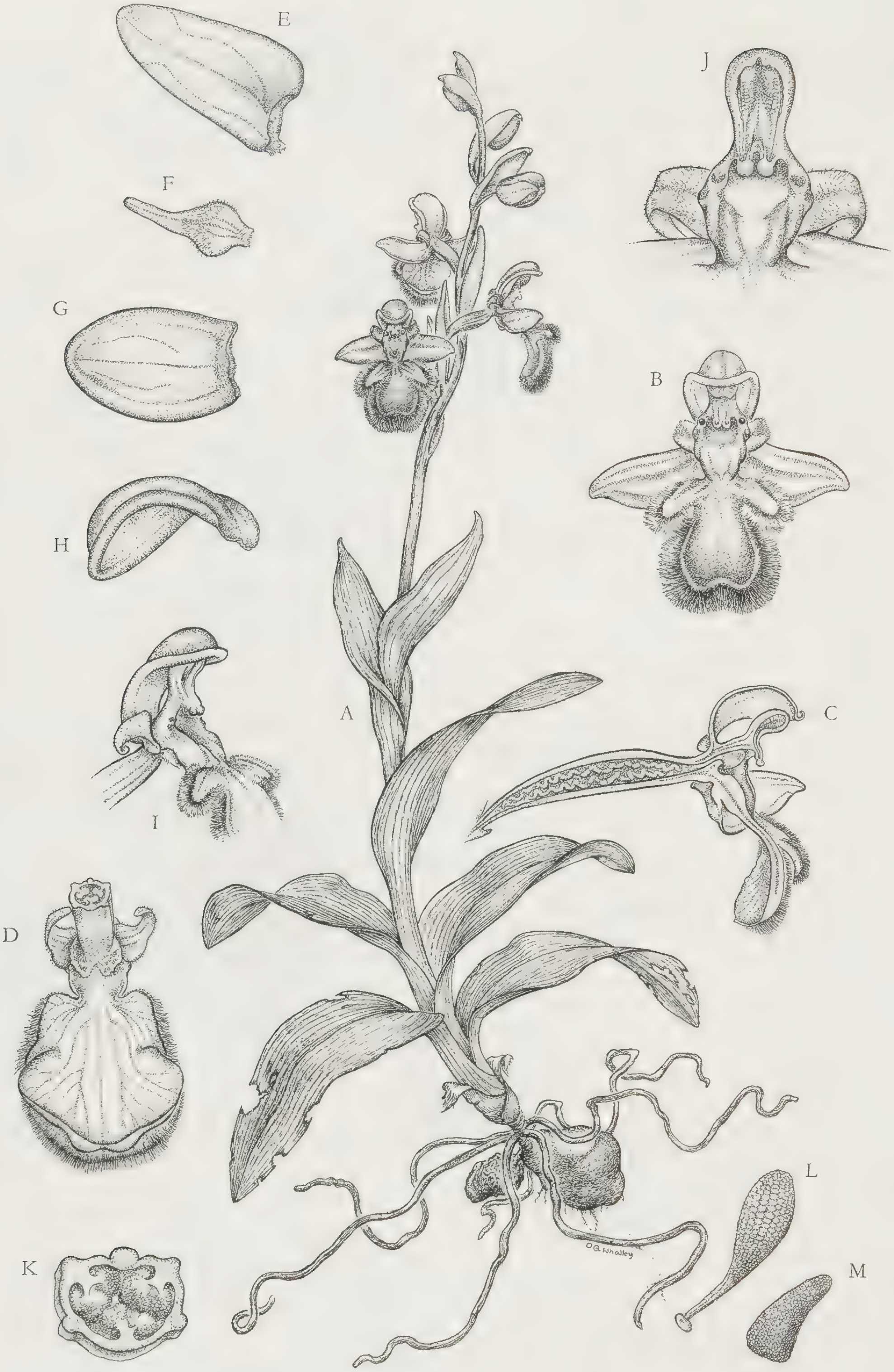

Fig. 88.1. *Ophrys speculum* Link. A. Habit, ×1; B. Flower from front, ×3; C. Flower with ovary, longitudinal section, ×3; D. Flower from back, sepals removed, ×3; E. Lateral sepal, ×4.5; F. Petal, ×4.5; G. Dorsal sepal, ×4.5; H. Dorsal sepal, oblique view, ×4.5; I. Flower from side, lateral sepals removed, ×3; J. Column, with petals behind, ×6; K. Ovary, transverse section, ×9; L. Pollinarium, ×9; M. Pollinium, ×45. Drawn by Oliver Q. Whalley from Kew Spirit Collection nos. 35081, 43657, and 43643.

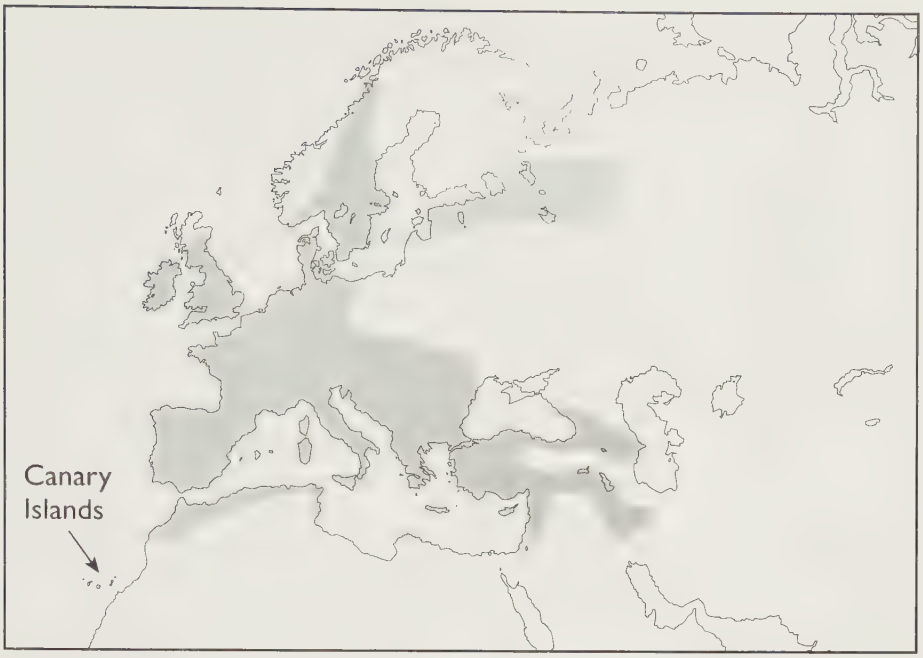

Fig. 88.2. Distribution map of *Ophrys*.

most species, is an often brightly coloured, shield-shaped area (basal field) at the base, and to either side of which may be two small swellings (basal callosities). *Column* having a short or rostrate, obtuse, acute or acuminate connective; rostellum minute; lateral appendages often indicated by coloured points, one on either side of the stigmatic cavity; pollinia two, attached to separate viscidia. *Ovary* sessile, not or slightly twisted, glabrous. **(JW)**

Distribution (Fig. 88.2)

A genus of approximately 126 species (Delforge 1995) distributed throughout Europe from the Canary Isles to the Caspian Sea, from southern Scandinavia south to North Africa, east to western Asia (NE Iran), attaining their greatest diversity in the Mediterranean Basin. The number of species listed by Delforge and others is undoubtedly inflated by the recognition of minor variants at specific rank. **(JW)**

Infrageneric treatment (PC, JW)

Nelson (1962) recognized seven sections as follows:

Ophrys section **Orientales** E. Nelson, *Mon. Ikon. Gattung Ophrys*, 133 (1962). Type species: *O. reinholdii* H. Fleischmann.

Ophrys section **Fuciflorae** Rchb.f., *Icon.* **XIII–XIV**, S. 85 ff. (1851). Type species: *O. holoserica* (Burm.f.) W. Greuter.

Ophrys section **Bombyliflorae** Rchb.f., *Icon.* **XIII–XIV**, S. 95 ff. (1851). Type species: *O. bombyliflora* Link.

Ophrys section **Araniferae** Rchb.f., *Icon.* **XIII–XIV**, S. 88 ff. (1851). Type species: *O. sphegodes* Miller.

Ophrys section **Arachnitiformes** E. Nelson, *Mon. Ikon. Gattung Ophrys*, 134 (1962). Type species: *O. arachnitiformis* Grenier & Philippe.

Ophrys section **Fusci-luteae** E. Nelson, *Mon. Ikon. Gattung Ophrys*, 134 (1962). Type species: *O. fusca* Link.

Ophrys section **Ophrys.** Type species: *O. insectifera* L.

Palynology

Schill and Pfeiffer (1977) examined 18 species of *Ophrys* and reported two types of sculpturing that characterized three groups of species: ± verrucose-hamulate in *O. attica* Soó, *O. bertolonii*, *O. biscutella*, *O. reinholdii* H. Fleischm., *O. speculum* Link, and *O. tenthredinfera*; laevigate-scabrate in *O. atrata* Lindl., *O. fuciflora*, *O. fusca*, *O. kurdica* D. Rückbr. & U. Rückbr., and *O. scolopax*; and intermediate forms of these in *O. apifera*, *O. garganica*, *O. lutea*, and *O. sphegodes*. Sculpture of *O. bombilifera* Link and *O. insectifera* varied greatly according to the provenance of material, but differences were not noted. **(AP)**

Cytogenetics

The genus *Ophrys* is characterized by a constant diploid chromosome number of $2n = 2x = 36$. The only exception is *Ophrys fusca*, having diploid ($2n = 2x = 36$) as well as tetraploid ($2n = 4x = 72$) karyotypes (Greilhuber and Ehrendorfer 1975). One specimen of *Ophrys tenthredinifera* from Italy was triploid with $2n = 3x = 54$ with three identical sets (Bianco *et al.* 1991). Cases of somatic aneuploidy with $2n$ = 37, 38, and 39 are also known (Greilhuber and Ehrendorfer 1975; Del Prete and Giordani 1978; Scrugli 1980; Corrias 1983). However, individuals of *Ophrys bertolonii* × *O. tarentina*, *O. apulica* × *bombyliflora* (Bianco *et al.* 1991), *O. biscutella* (unpublished), *O. holoserica* (Burm.f.) Greuter subsp. *pollinensis* E. Nelson ex O. Danesch & E. Danesch, and *O. promontorii* (Greilhuber and Ehrendorfer 1975) have evidence of supernumerary chromosomes in both somatic metaphases and in germ cells during meiosis. Numerous karyological observations indicated that aneuploidy occurs preferentially in hybrid individuals or species of hybrid origin.

The 'basic' karyotype of *Ophrys* generally shows three pairs of chromosomes with satellites, the first of which is characterized by a long satellite on the short arm of a metacentric or submetacentric chromosome (Fig. C.2c). A marked variation in morphology and size of the long satellite has been noted within *Ophrys* (Bianco *et al.* 1989*b*, 1991). Bianco *et al.* (1991) reported the karyotype of *Ophrys tenthredinifera* having five pairs of chromosomes with satellites. However, the long satellite described above does not appear on the short arm but on the longer arm of a metacentric chromosome. In *O. tenthredinifera*, examination of several somatic plates revealed one chromosome showing secondary constriction on the short arm and a few microsatellites on the long arm, which resemble the ones observed in *Anacamptis* species (D'Emerico, unpublished).

The karyotypes of *Ophrys* taxa can be arranged in a series showing a progressive trend from symmetrical (more metacentric chromosomes) to asymmetrical (more submetacentric chromosomes) karyotypes. Karyotypes with a high number of metacentric chromosomes are present in *Ophrys bombyliflora* and *O. fusca*. On the other hand, a high number of submetacentric chromosomes has been observed in *O. insectifera* and *O. bertolonii*. In the *O. fusca*–*O. lutea* group, *O. lutea* and *O. sicula* (=*O. lutea* subsp. *minor* (Todaro) O. Danesch & E. Danesch) have the same number of metacentric and submetacentric chromosomes (Bianco *et al.* 1989*b*). Moreover, these taxa have similar complements to *O. fusca*, showing an evidently close relationship as confirmed by phylogenetic analysis using ITS sequences (Pridgeon *et al.* 1997).

In karyotypes of interspecific hybrids, meiosis at metaphase I is completely normal, again indicating the close homology between parental genomes. However, univalents, trivalents, or supernumerary chromosomes were observed in some hybrids (Bianco *et al.* 1991).

The application of the C-banding technique to the species of *Ophrys* examined revealed that all species possess small centromeric bands (Fig. C.4c). However, some taxa showed chromosomes characterized by telomeric and subtelomeric bands. Using this technique it is possible to show that species belonging to different sections of this genus differ in the amount of total heterochromatin. **(SD)**

Phytochemistry

The phenolic glucoside loroglossin was isolated from *O. apifera* (Delauney 1921*a*,*b*), *O. insectifera* (Delauney 1923*a*,*b*), and *O. sphegodes* (Delauney 1920; 1921*a*,*b*,*c*). Its structure was later determined to be *bis*[4-(β-D-glucopyranosyloxy)benzyl] *erythro*isobutyltartrate by Aasen *et al.* (1975; Fig. 81.4).

The leaves of *O. apifera*, *O. bombyliflora*, and *O. tenthredinifera* contain the flavonols kaempferol and quercetin. These flavonol aglycones were detected in acid-hydrolysed extracts of leaf tissue, indicating that they originate from flavonol *O*-glycosides (C. A. Williams 1979). Uphoff (1979) investigated the anthocyanin content of the flowers of several *Ophrys* species, and a more comprehensive survey was published subsequently by Strack *et al.* (1989). This showed that cyanidin 3-glucoside (chrysanthemin) and cyanidin 3-oxalylglucoside (ophrysanin) are the most abundant anthocyanins in *Ophrys* and the main pigments of the labella. The site of acylation by oxalic acid in ophrysanin is at C-6 of the 3-glucoside (Strack *et al.* 1986). The major anthocyanins in petals and sepals are the more complex cyanidin oxalylglucosides such as serapianin and orchicyanins I and II, e.g. in *O. holoserica, O. phrygia,* and *O. straussii.* Borg-Karlson (1990) reviewed the chemical composition of volatiles from the flowers of 30 *Ophrys* taxa and from the insects attracted to them.

Baytop and Sezik (1968) reported on the chemical analysis of tubers of *O. fuciflora* and *O. fusca* collected in south-west Anatolia, Turkey. Their results were summarized in a later review by Ernst and Rodriguez (1984). See *Anacamptis*. **(NV**, **RG)**

Ecology

The majority of *Ophrys* orchids grow on calcareous soils, such as those derived from chalk and limestone which are alkaline, relatively warm and dry, and nutrient-poor (Delforge 1995). In the British Isles, *O. sphegodes* in southern England primarily occurs on chalk in Sussex and Kent, on the Purbeck limestones in Dorset, and on oolitic and Liassic limestones in Northamptonshire (Summerhayes 1951; Hutchings 1987). Only a few species in the genus also sometimes occur on more acidic soils, for example *O. scolopax* and *O. tenthredinifera* and/or on more wet ones, such as *O. bombyliflora* and *O. insectifera* (Davies *et al.* 1988; Delforge 1995). Since orchids such as *O. sphegodes* and *O. insectifera* can tolerate a wider range of soil pH and moisture conditions in the Mediterranean region, it has been suggested that their restriction to chalk and limestone soils in the northern parts of their ranges is advantageous in promoting their growth and survival in the cooler and damper climates of northern Europe (Summerhayes 1951).

In the Mediterranean, *Ophrys* species grow most frequently in maquis or garrigue shrublands and unimproved grasslands and fallow fields (Delforge 1995). In Britain, *Ophrys* plants are typically found growing in open grasslands such as on the chalk downs of south-east England, where the turf is short (Summerhayes 1951; Lang 1989). The recent National Vegetation Classification of the British Isles cited the calcicolous grassland type as including *O. fuciflora* and *O. sphegodes* as well as other rare orchids such as *Orchis simia* Lam., *Neotinea ustulata*, and *Orchis anthropophora* (L.) All. (Rodwell 1992). Hutchings (1989) suggested for *O. sphegodes* in Sussex that such chalk grassland is a sub-optimal refuge habitat because its populations require careful habitat management for their survival, as the species can quickly be eliminated from ungrazed or fertilized sites through competition from other plants. Most *Ophrys* species prefer to grow in full sunlight but can tolerate partial shade and often grow in olive groves and open woods of pine, oak, and beech. *Ophrys insectifera* is unusual in that it frequently grows in dense woodlands in heavy shade, for example in the beechwoods of the North and South Downs in southern England (Summerhayes 1951; Lang 1989), although it does grow in more open habitats, such as among the limestone pavement of the Burren on the west coast of Ireland and in the peat bogs of the Central Plain with other marshland orchids such as *Epipactis palustris* and *Gymnadenia conopsea* (Summerhayes 1951). Man-made habitats, including disused quarries, railway embankments, and roadside verges, are other typical *Ophrys* habitats. Wells and Cox (1991) suggested that *O. apifera* behaves as a pioneer species because it is one of the earliest colonizers of bare or disturbed ground. It also grows on stabilized or semi-stabilized sand-dunes (Summerhayes 1951), and several other species often grow near the coast (e.g. *O. sphegodes* in England). In continental Europe, *Ophrys* species can grow at an elevation of 2000 m, although most species grow at mid-elevations of 800–1400 m (50% of the 126 *Ophrys* species listed by Delforge (1995) grew at mid-elevations compared with 32% at a range of 200–700 m).

Ophrys species flower in the spring in the Mediterranean, usually from March to May. In northern Europe, flowering in the summer is more common, as with *O. insectifera* (in May/June) and *O. apifera* (in June/July) (Delforge 1995). Within these flowering periods, individual *Ophrys* flowers are relatively long-lived (Summerhayes 1951) and can remain open for several weeks if they have not been pollinated (Neiland and Wilcock 1995). As the flowers reach anthesis, the basal rosette normally starts to senesce. These leaves emerged above ground in the previous autumn and remained green throughout the winter ('winter-green' orchids). Following complete senescence of the aerial stem at the end of the spring or summer, the plant remains underground as a tuber for several weeks or months, an adaptation that enables *Ophrys* species to avoid desiccation during the dry summer of the Mediterranean.

Tubers and roots of *Ophrys* species are replaced every year. Observations made of *O. apifera* in England (Wells and Cox 1989) and *O. sphegodes* in Belgium (Delforge 1995) showed that new tubers begin to develop in November and can be seen as small white protuberances on the stem above the old tuber. During the winter, growth of the new tuber is slow, but in the spring it begins to increase in size rapidly. By the time the plant flowers, the new tuber may be as large or even larger than the old one, which shrivels as its food reserves are utilized in the formation of the flowering stem and new tuber. After flowering and senescence of the aerial parts, the old tuber has been completely re-absorbed and the new tuber becomes upright. By the early autumn, a new shoot has developed at its top, from which the new vegetative or flowering stem will develop.

The proportion of plants that flower in a population in any one year varies considerably between *Ophrys* species. In two long-term demographic studies in southern England, the average frequency of plants flowering in *O. apifera* was 27.4% and in *O. sphegodes* 83.7% (Hutchings 1987; Wells and Cox 1989). The probability of *Ophrys* plants flowering is influenced by characteristics such as tuber size and leaf number. For example, Wells and Cox (1989) found a highly significant difference in all plant characters measured in a study of *O. apifera* between plants going to flower and those going to remain vegetative. Plants that were going to flower in June had more leaves, a larger leaf area, more roots, larger tubers, and a greater total dry weight at four sampling times (November, March, May, and June) than plants that remained vegetative. Leaf characters (total rosette leaf area, leaf number, or length of longest leaf) were found to be particularly useful in predicting the probability of flowering in *O. apifera*. All plants that flowered had at least two leaves in mid-May; in plants with more than two leaves the probability of flowering increased with increasing rosette size.

The number of leaves in a rosette depends not only on the age of the plant and therefore the resources available from the tuber but also on the seasonal emergence time. Wells and Cox (1989) found that plants of *O. apifera* that appeared above ground first tended to be those that eventually had the largest number of leaves, whereas plants that emerged later had fewer and smaller leaves. Weather conditions such as low rainfall may delay emergence time in the autumn (Rasmussen 1995). Drought can also prevent infloresence formation (Wells and Cox 1989) or cause premature floral senescence (Neiland 1994), thereby reducing the likelihood of successful pollination and seed set in *Ophrys* species.

Fruit-set in *Ophrys* species is often low; for example 7.6% and 21.3% of flowers produced seed capsules in populations of *O. vernixia* Brot. and *O. bombyliflora*, respectively, in Portugal (Neiland 1994). An average of 8.7% was found among populations of *O. insectifera* studied in England, Germany, and Denmark (Neiland and Wilcock 1998). *Ophrys apifera* is exceptional in that most flowers set fruit throughout its range, but this high level of reproductive success is achieved by self-pollination. *Ophrys* capsules are usually large and may contain 10 000–15 000 seeds (Salisbury 1942; Neiland 1994), which is more than many other European orchid genera (Neiland and Wilcock 1995). Some germination of seeds has been observed in the field in spring (Fabre 1856; Fuchs and Ziegenspeck 1927, cited in Rasmussen 1999). It has often proved difficult to germinate seeds asymbiotically (Veyet 1969; Rasmussen 1995), although Möller (1985) successfully germinated and grew seedlings of *O. holoserica* from seed. Some fungal endophytes (*Tulasnella* sp.) have been found to be effective in symbiosis with *Ophrys* (Clements *et al.* 1986), and others have been isolated from the roots and identified as *Eupulorhiza* spp. (Andersen 1990, cited in Rasmussen 1995). Observations in the field indicate that following protocorm growth, formation of a tuber precedes leaf development (Rasmussen 1995). With *O. apifera* the first leaf is usually produced in the second year after germination, but the plant may remain in a vegetative state for an additional one to six years before flowering takes place (Wells 1981). *Ophrys sphegodes*, growing at the edge of its European range in southern England, is unusual in that time to flowering is short, with over 70% of plants flowering in the first year that they emerge above ground (Hutchings 1989).

Some *Ophrys* species have been reported to be monocarpic and show irregular patterns of appearance in particular localities

(Summerhayes 1951). Recent demographic studies, however, demonstrated that *Ophrys* plants often have a period of dormancy during their lives, but that they can flower (and fruit) for several years in succession (Hutchings 1989; Wells and Cox 1991). In a study of *O. sphegodes* in Sussex in southern England, approximately 50% of the population was estimated to be dormant in any one year, and individuals could remain dormant for up to two years before re-emerging above ground (Hutchings 1987). Some orchids in the population had life spans of at least 10 years, but most were short-lived (half-lives of cohorts ranged from 1.5–2.3 years). Therefore, although the species is capable of producing fruit more than once, individual plants in the population are effectively monocarpic because they may flower only once before dying. By contrast, in a study of *O. apifera* in Cambridgeshire, the average half-life for the population was 6.6 years, and it was estimated that 64% of the population was more than eight years old (Wells and Cox 1981). Regular seed production is likely to be particularly important for the maintenance of populations, especially those with short half-lives or at the edge of the range where environmental conditions may be sub-optimal, because vegetative propagation through multiplication of the tubers is insignificant in *Ophrys*. For example, Hutchings (1987) estimated that <5% of *O. sphegodes* plants propagated vegetatively per annum. Given this dependence on seed input for population maintenance, conservation management practices that aim to reduce the mortality of flowering plants and encourage a high level of recruitment of new plants are likely to be most successful in conserving rare or threatened *Ophrys* populations (Hutchings 1989; Waite and Hutchings 1991).

Ophrys includes many species with localized distributions that are rare and threatened, including some listed as Red Data Book plants. A few species have been the focus of conservation programmes. For example, in Britain, *O. sphegodes* has been included in a wardening scheme to prevent it being collected from the wild (Farrell and Fitzgerald 1989). Favourable grazing management regimes have been successfully adopted at some locations to encourage seed recruitment and increase population sizes (Hutchings 1989; Waite and Hutchings 1991). However, across the range of the genus there are potential threats to the survival of *Ophrys* species. In a recent survey for the IUCN (IUCN Orchid Specialist Group 1996), Delforge cited overgrazing, coastal and inland tourist development, agriculture, urbanization, land drainage, gathering of tubers for salep, forestry, and general destruction of the habitat as serious threats and also assesses the risks of extinction as medium to high for many of the most threatened species, especially where populations are small. **(RN)**

Pollination

Flowers of the genus *Ophrys* are pollinated by sexual deception, a pollination system that is unique to Orchidaceae (Nilsson 1992). Pouyanne (1917) and Godfery (1925) were the first to interpret correctly the behaviour of male solitary bees on *Ophrys* flowers. Later, detailed studies by the groups of Kullenberg (Kullenberg 1961, 1973; Kullenberg and Bergström 1976*a*, *b*; Kullenberg *et al.* 1984) and Borg-Karlson (Borg-Karlson *et al.* 1987; Borg-Karlson and Groth 1986; Borg-Karlson 1990; Borg-Karlson *et al.* 1993) revealed that flowers imitate female hymenoptera in colour, morphology, and scent. The floral scent is highly specific (Borg-Karlson *et al.* 1993; Schiestl *et al.* 1999). Males of solitary bees, which often emerge earlier than females, are attracted to the female-mimicking flowers. After landing on the hairy labellum, males try to copulate with the labellum, a process called pseudocopulation. Pollinaria are then attached to either the head or abdomen of the pollinator. Depending on the specificity of the pollinator attraction, this pollination system may provide a strong prezygotic barrier to gene flow and may thus explain why multiple *Ophrys* species may flower in sympatry and during the same flowering period despite the lack of strong postzygotic barriers (Paulus and Gack 1990). Although most species are pollinated by male solitary bees, a few notable exceptions exist. Some species, such as *O. insectifera* and *O. speculum* are pollinated by male wasps, and *O. chestermanii* (J. J. Wood) P. Gölz & H. R. Reinhard, a species endemic to Sardinia, is pollinated by males of the cuckoo bumble-bee *Psithyrus vestalis* (Paulus and Gack, 1995). **(AW, SC, AD)**

Uses

Tubers of several species are used in eastern Mediterranean countries and parts of the Middle East for the production of salep. **(JW)**

Cultivation

Ophrys species often occur in open habitats on calcareous soils. They are recommended for pot culture in the alpine house in compost C with added lime. Plants may appear spontaneously in gardens and can be naturalized by careful mowing regimes. **(CB)**

Taxonomic notes

This genus, above all others in subtribe Orchidinae, has been the subject of much attention in recent years with the result that the number of new taxa has virtually trebled, adding to an already unwieldy and confusing nomenclature. It seems that, in many cases, natural infraspecific variation has been ignored as such, and unnecessary splitting using minor differences between populations has occurred. Many of the confusing new taxa proposed in (for example) the *O. fusca/lutea*, *O. scolopax*, and *O. sphegodes* groups seem to be artificial and merely extremes in a cline of variation. On the other hand, several recently recognized taxa do appear to be isolated by flowering time and pollinator specificity.

Delforge (1995) considered the genus to be monophyletic, close to *Serapias*, but probably derived from *Orchis*. He recognized two monophyletic sister groups defined by the position that the pollinator adopts on the lip during pseudocopulation: sect. *Pseudophrys* Godfery, equivalent to Nelson's sect. *Fusci-luteae*, in which the pollinia are carried away by the insect's abdomen, include the *O. fusca/lutea* and *O. omegaifera* groups; and sect. *Ophrys* (as *Euophrys*), in which the pollinia are removed by the head of the insect, include all the remaining complexes and groups within the genus.

The complex and highly specialized pollination syndromes involving male insects of several different genera has provided a strong selective pressure. Adaptive radiation has no doubt worked in parallel with pollinators. Although intergeneric hybridization is unknown, effective genetic breeding barriers do not seem to exist, and interspecific hybridization is widespread in the wild. Hybrid fertility is high, and consequently many of the 'species' currently recognized may be of hybrid origin.

Section *Fusci-Luteae* (*Pseudophrys*) shares several floral morphological characters with *Orchis* from which Delforge considered it to be probably derived. He suggested that these have become modified in section *Ophrys*, derived from '*Pseudophrys*', during the evolution toward head pollination (see Delforge 1995). Within sect. *Ophrys*, he recognized five trends comprising the *O. insectifera*, *O. speculum*, *O. holoserica* (*O. fuciflora*), *O. argolica*, and *O. sphegodes* groups, the first two being self-contained and probably only distantly related, and last three more specialized, closely related complexes. **(JW, PC)**

Taxonomic literature

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89. ORCHIS

Orchis L., *Sp. Pl.*, ed. 1, 939 (1753). Type species: *Orchis militaris* L.

Abrochis Neck., *Elem.*, **3**, 130 (1790). Type species: Not indicated.

Zoophora Bernh., *Syst. Verz. Erf.*, 308 (1800). Type species: Not indicated.

Strateuma Salisb., *Trans. Hort. Soc.*, **1**, 290 (1812). Type species: *Orchis militaris* L.

Aceras R. Br., in Aiton, Hort. Kew, ed. 2, 5, 191 (1813). Type species: *Aceras anthropophorum* (L.) W. T. Aiton.

Derivation of name

From the Greek *orchis*, testicle, referring to the appearance of the tubers. **(JW)**

Description (Plate 108; Fig. 89.1)

Small to medium sized *herbs*. *Rootstock* tuberous, tubers two (sometimes three), globose, ovoid or ellipsoid, entire, sessile or stipitate. *Stem* glabrous. *Leaves* basal, rosulate, spotted or unspotted. *Inflorescence* cylindrical, sparsely to densely flowered, enclosed in a sheathing spathe-like leaf when emerging; floral bracts usually thin, membranous, never leafy, often coloured. *Flowers* in various shades of red, purple, pink or yellow, rarely greenish yellow, reddish brown or white, often scented. *Dorsal sepal* usually erect, free. *Petals* entire, free, usually porrect. *Lateral sepals* spreading, erect or connivent with dorsal sepal and petals to form a hood, all glabrous. *Labellum* decurved, three- or apparently four-lobed, mid-lobe entire or divided into lobules, glabrous or ± papillose above, spurred, rarely spurless, spur filiform or saccate, disc with or without basal calli. *Column* short, erect; rostellum three-lobed, folded median lobe placed between parallel anther loculi; pollinia two, each with a caudicle attached to separate viscidium or, rarely, connate viscidia enclosed in a single, often bilobed bursicle. *Ovary* cylindrical, sessile, twisted, glabrous. **(JW)**

Distribution (Fig. 89.2)

About 33 species distributed in Europe, particularly the Mediterranean region, temperate Asia, and North Africa, from the Azores, Madeira, and Canary Islands in the west to Iran and the Caucasus in the east, north as far as Scandinavia. **(JW)**

Labellointegrae and *Coriophorae* are now included in *Anacamptis*.

Infrageneric treatment (JW)

The following sections were recognized by Schlechter (1926) and Vermeulen (1949, 1972)

Orchis section **Labellointegrae** Verm., *Ned. Kruidk. Arch.*, **56**, 236 (1949). Type species: not designated.

Orchis section **Labellotrilobatae** Verm., *Ned. Kruidk. Arch.*, **56**, 236 (1949). Type species: not designated.

Orchis section **Coriophorae** Parl., *Fl. Ital.*, **3**, 468 (1858). Type species: *Orchis coriophora* L.

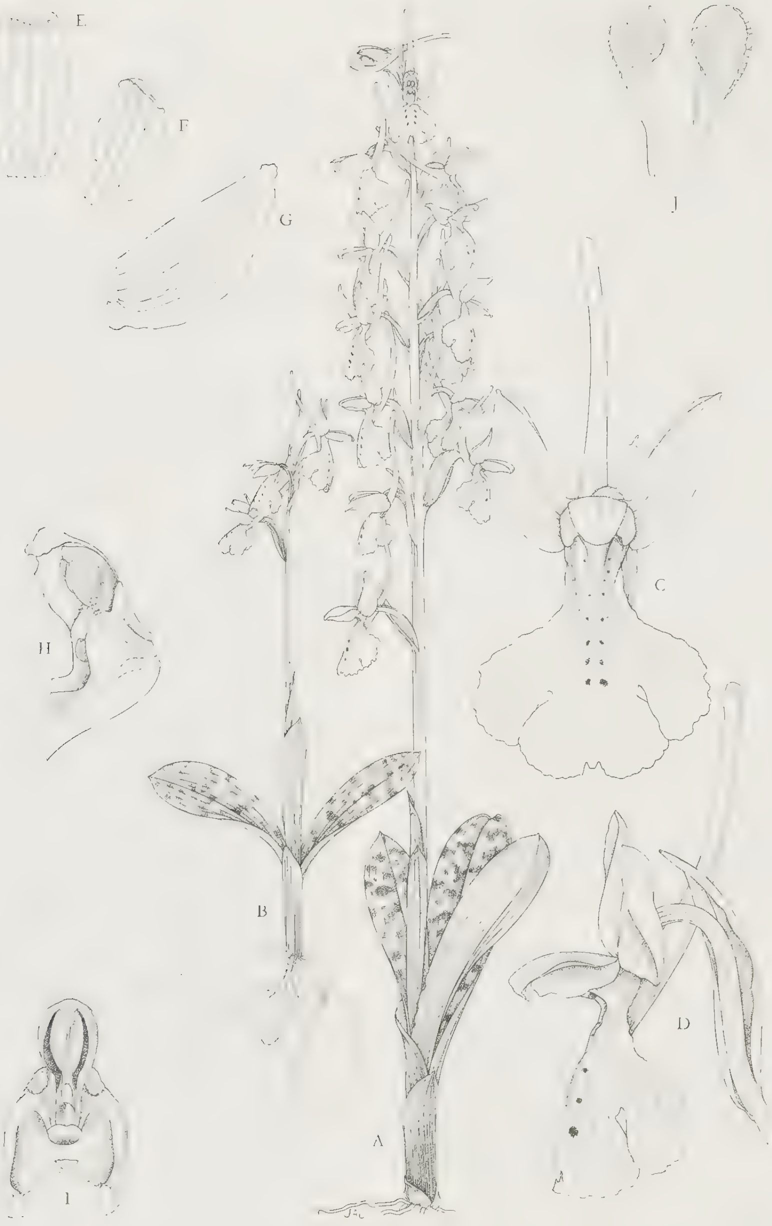

Fig. 89.1. *Orchis troodi* (Renz) P. Delforge. A. Habit, ×0.8; B. Habit, ×1.2; C. Flower, front view, ×1.4; D. Flower, side view, ×1.4; E. Dorsal sepal, ×2.3; F. Petal, ×2.3; G. Lateral sepal, ×2.3; H. Column, side view, ×2.5; I. Column, front view, ×2.5; J. Pollinaria, ×7.3. Drawn by Joanna A. Langhorne from *Wood 90*, *Meikle 2260*, and *Merton 2870*.

Orchis section **Militares** Parl., *Fl. Ital.*, **3**, 471 (1858). Type species: not designated.

Renz (1978) preferred to follow the sectional treatment proposed by Schlechter (1926):

Orchis section **Andranthus** Schltr., in Keller & Schltr., *Feddes Repert. Sonderbeih.* **A**, **1**, 159 (1926). Type species not designated.

Orchis section **Coriophoranthus** Schltr., in Keller & Schltr., *Feddes Repert. Sonderbeih.* **A**, **1**, 159 (1926). Type species not designated.

Orchis section **Heteranthus** Schltr., in Keller & Schltr., *Feddes Repert. Sonderbeih.* **A**, **1**, 159 (1926). Type species not designated. Treated under sect. *Orchis* by Renz.

Orchis section **Morianthus** Schltr., in Keller & Schltr., *Feddes Repert. Sonderbeih.* **A**, **1**, 159 (1926). Type species not designated.

Orchis section **Phalaeanthus** Schltr., in Keller & Schltr., *Feddes Repert. Sonderbeih.* **A**, **1**, 159 (1926). Type species not designated.

Of the sections recognized by Schlechter, *Andranthus* contains several taxa now included in *Anacamptis*, and *Heteranthus* includes a few taxa now included in *Neotinea*. All of the taxa Schlechter included within *Coriophoranthus*, *Morianthus*, and *Phalaeanthus* are referable to a recently expanded *Anacamptis*. Vermeulen's sections *Labellointegrae* and *Coriophorae* are now included in *Anacamptis*. **(JW)**

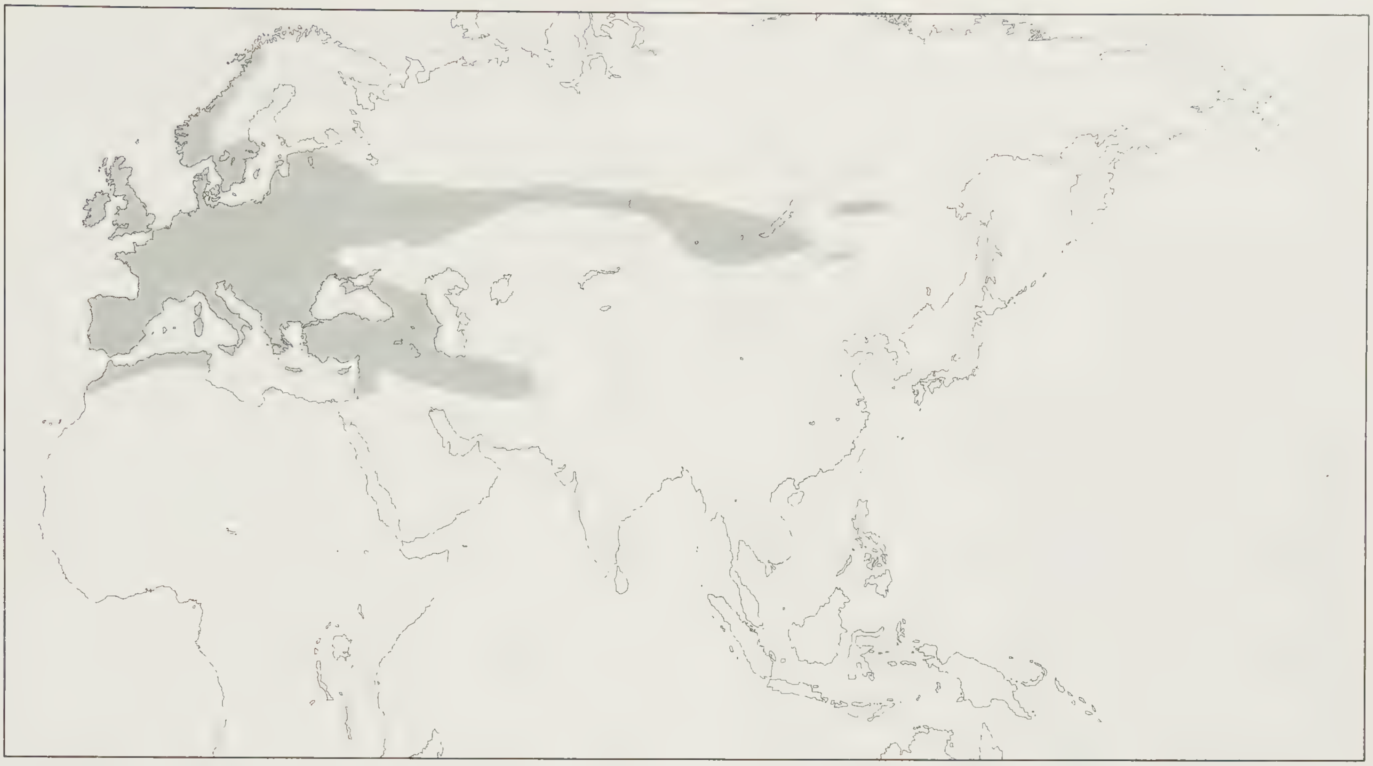

Fig. 89.2. Distribution map of *Orchis*.

Palynology

Some species of *Orchis* are heterogeneous in pollen morphology, particularly *O. mascula* and *O. militaris* (Schill and Pfeiffer 1977). Sculpturing of *O. mascula* may be laevigate-scabrate, laevigate-perforate, verrucose-hamulate, ornate or baculate-pilate. *Orchis militaris* may have ornate, baculate-pilate, hamulate or reticulate-heterobrochate sculpturing, and *O. anatolica* may have laevigate-perforate, verrucose-hamulate or hamulate sculpturing. Other species are more consistent in this feature: laevigate-scabrate in *O. pallens* L.; hamulate in *O. quadripunctata*; reticulate-heterobrochate in *O. purpurea*; and baculate-pilate in *O. italica*. *Orchis anthropophora* (reported as *Aceras anthropophorum*) has reticulate sculpturing with interrupted muri, a trait that seems to be expressed in infrageneric hybrids (Schill and Pfeiffer). **(AP)**

Cytogenetics

Most cytological studies of *Orchis* have resulted in a chromosome number of $2n = 2x = 42$. The exceptions are *Orchis patens* subsp. *patens* with $2n = 4x = 84$ (recently confirmed; D'Emerico *et al.*, unpublished) and *O. patens* subsp. *canariensis* (Lindl.) Rchb.f. with $2n = 80$ (Hautzinger 1978), but unconfirmed and presumably classifiable as $2n = 84$). One rare case of triploidy has been observed in *Orchis italica* with chromosome number $2n = 3x = 63$ (Bianco *et al.* 1991). There is a strong similarity in the karyomorphology of *Orchis* to that of *Neotinea*.

In *Orchis* there is surprising variation in distribution and content of heterochromatin. Preliminary analysis of *O. italica* (Fig. C.2e), *O. militaris*, *O. purpurea*, and *O. simia* showed similar results with C-banding. None of these species possesses stainable heterochromatin, at least with the techniques utilized. However, the C-banding of *Orchis provincialis* subsp. *provincialis* revealed numerous chromosome pairs with thin centromeric heterochromatin and two with smaller telomeric bands. By contrast, C-banding of *O. mascula* subsp. *mascula* showed chromosomes with very thick centromeric heterochromatin and chromosomes with thin centromeric bands (D'Emerico *et al.*, unpublished). **(SD)**

Phytochemistry

The phytochemistry of this genus is closely linked to the development of the concept of phytoalexins, a subject that has been reviewed in detail elsewhere (Arditti 1979; Stoessl and Arditti 1984). These defence compounds were first detected by Bernard (1911) during the course of his investigations into infection of *Anacamptis morio* (cited as *O. morio*) and *Himantoglossum hircinum* (cited as *Loroglossum hircinum*) tubers by *Rhizoctonia repens*. The first orchid phytoalexin to be characterized, orchinol, was obtained from tubers of *O. militaris* infected with *R. repens* (Boller *et al.* 1957). Its structure was solved using a combination of spectroscopic methods and chemical synthesis as 2,4-dimethoxy-7-hydroxy-9,10-dihydrophenanthrene (reviewed in Stoessl and Arditti 1984; see also Fig. 81.3). A second orchid phytoalexin, hircinol (4-methoxy-2,5-

dihydroxy-9,10-dihydrophenanthrene), was detected in trace amounts in *O. militaris* (Urech *et al.* 1963). Infection of the tubers of *O. anthropophora* (cited as *Aceras anthropophorum*) and *O. mascula* with a strain of *Rhizoctonia repens* from *O. militaris* also resulted in the synthesis of orchinol and *p*-hydroxybenzylalcohol. This observation was made as part of a survey of orchinol and *p*-hydroxybenzylalcohol production in a number of species representing genera in subtribe Orchidinae (Nüesch 1963; Gaumann *et al.* 1960). Possible biosynthetic routes to orchinol were reviewed comprehensively by Stoessl and Arditti (1984).

The phenolic glucoside loroglossin was isolated from *O. mascula* (Delauney 1923*a*, *b*; Karrer and Matter 1947), *O. militaris*, *O. purpurea* (Delauney 1923*a*, *b*), and *O. simia* (Delauney 1921*a*, *b*). Its structure was later determined to be *bis* [4-(β-D-glucopyranosyloxy)benzyl] *erythro*isobutyltartrate by Aasen *et al.* (1975). A second, structurally related glucoside was isolated from *O. militaris* and characterized as *bis* [4-(β-D-glucopyranosyloxy)benzyl]-(*R*)-2-isobutylmalate (Aasen *et al.* 1975; Fig. 81.4). The presence of coumarin glucosides in *O. anthropophora*, *O. militaris*, *O. purpurea*, and *O. simia* was suggested from the observation that extracts of these species subjected to either acid hydrolysis or treatment with emulsin yielded free coumarin (Hérissey and Delauney 1922).

The leaves of *O. italica* contain quercetin, whereas the leaves of *O. anthropophora* and *O. mascula* contain both quercetin and kaempferol. These flavonol aglycones were detected in acid-hydrolysed extracts of leaf tissue, indicating that they originate from flavonol *O*-glycosides (C. A. Williams 1979). Uphoff (1979) and Strack *et al.* (1989) investigated anthocyanin content in the flowers of more than 20 *Orchis* species. All contain cyanidin glucosides, principally the 3-glucoside (chrysanthemin), 3,5-diglucoside (cyanin), 3,7-diglucoside (seranin), 3-oxalylglucoside (ophrysanin), oxalyl-3,7-diglucoside (serapianin), oxalyl-3,5-diglucoside (orchicyanin II), and oxalyl-3,5-diglucoside-kaempferol 7-glucoside (orchicyanin I, an intramolecular copigment). The site of acylation by oxalic acid is known only for ophrysanin (C-6 of the 3-glucoside) (Strack *et al.* 1986).

Baytop and Sezik (1968) reported on the chemical analysis of tubers of *Orchis* species collected in south-west Anatolia, Turkey. Their results were summarized in a later review by Ernst and Rodriguez (1984). The species analysed were *O. anatolica*, *O. italica*, *O. mascula* subsp. *pinetorum* (cited as *O. pinetorum*), and *O. simia*. See *Anacamptis*. **(NV, RG)**

Ecology

Members of the widespread Eurasian genus *Orchis* occur in a variety of habitats including grassland, shrubland, and deciduous or coniferous woodland, and usually grow in well-drained calcareous soils such as those derived from chalk and limestone (Sundermann 1962, cited in Rasmussen 1995; Pettersson 1976; Dafni 1987; Davies *et al.* 1988; Lang 1989; Delforge 1995). Among prime examples of calcicoles in the group are the Mediterranean orchids, *O. italica* and *O. quadripunctata*, which grow on dry, stony calcareous soils in maquis and garrigue shrublands and open pinewoods in southern Europe (Davies *et al.* 1988; Delforge 1995). Similarly, many *Orchis* species growing in Britain are calcicolous, only occurring on chalk and limestone substrates. For example, all records of the now rare species, *O. simia*, have been from chalk in England, wheras *O. anthropophora* is found in both chalk downland in Kent and Surrey and in grassland on oolitic or Liassic limestone in Northamptonshire, Lincolnshire, and Somerset (Summerhayes 1951). Likewise, the soils from the four remaining sites of *O. militaris* in southern England are all chalk rendzinas with high calcium carbonate levels, a pH >7.5, and free drainage (Farrell 1985). Soils are similar from sites with *O. purpurea*, another rare British species confined to scrub and beechwoods on chalk in the south-east of England (Rose 1948). These soils typically dry rapidly due to their porosity, show rapid decay of the humus layer (within about one year) and are alkaline throughout their profile from the soil surface to orchid-rooting depth (Rose 1948).

In continental Europe, some *Orchis* species can occupy a wider range of habitats and soil types than in England. *Orchis militaris*, for example, grows on calcareous to neutral soils throughout its distribution, but in mainland Europe it also appears on wetter soils such as marls, peats, and dune sand (Summerhayes 1951), and in central parts of its range (in Sweden, Lithuania, Poland, Germany, Austria, Hungary, and the Crimea) it is often reported from wet meadows (Farrell 1985). *Orchis* species also grow at higher elevations on the Continent than in Britain where they are typically lowland plants. *Orchis militaris*, which grows at 15 m in Suffolk and 183 m in the Chiltern Hills, is found from sea level in the Netherlands to 1800 m in the French Department of Isère (Farrell 1985), whereas *O. mascula* is reported at up to 3000 m in the Alps (Davies *et al.* 1988; Delforge 1995). Chalk and limestone soils are comparatively warm and dry, and it has been suggested that the restriction of many *Orchis* species to these soils in England is due to their ameliorating effect for orchid growth in the cool and damp climate of the British Isles (Summerhayes 1951). Habitats in England, at the north-western limits of the range of the genus, may still be sub-optimal for *Orchis* (Hutchings 1989). The preference of many *Orchis* species for calcareous soils in the Mediterranean has alternatively been explained as a consequence of the low-competitive ability of these species such that they are only able to exploit successfully habitats in which there is little competition from other plants (Dafni 1987). The typical calcareous maquis and garrigue shrublands in which many *Orchis* species grow in the Mediterranean region are nutrient-poor because of the high pH levels of the soil and are consequently characterized by the relative scarcity of annuals and geophytes. Dafni (1987) suggested that, because of their mycorrhizal associations and characteristic adaptations for growth in disturbed areas (cf. Sanford 1974), *Orchis* species and other terrestrial orchids of the Mediterranean region are able to thrive in such nutrient-poor and disturbed environments where other plants cannot. One exception in the genus is the widespread species, *O. militaris*, which is absent from much of the Mediterranean because of its intolerance for hot, dry summers and largely confined to mountain localities in the region (Farrell 1985).

Some *Orchis* species frequently grow on non-calcareous soils in addition to alkaline ones. For example, *O. anatolica* growing in eastern Mediterranean regions sometimes occurs on more neutral substrates, whereas *O. sitiaca* (Renz) P. Delforge, a species endemic to Crete, can occur on slightly acid soils (Delforge 1995). Of the more widespread Eurasian species, *O. mascula* is notable because of the diversity of habitats and variety of soil types in which it typically grows. Although it prefers alkaline substrates to acid or wet ones, it does grow in neutral to slightly acid situations in habitats ranging from chalk grassland to deciduous woodland and from coastal sand-dunes to mountain cliffs. For example, in southern England *O. mascula* occurs in large numbers on the grassy slopes of the chalk downs but is also a frequent inhabitant of coppiced woods of oak, ash, and beech (Summerhayes 1951; Sanford 1991). Similarly, Nilsson (1983*a*) noted that *O. mascula* commonly occurs on the Swedish island of Öland in both open dry meadows in the limestone alvar and in shaded hazel groves. The widespread appearance of *O. mascula* in limestone pavements on coastal sand-dunes and cliff tops and on rocky mountain ledges indicates that it is also able to grow in soils that are relatively shallow (Summerhayes 1951; Lang 1989; Allan *et al.* 1993) and at a range of elevations from sea level up to 2650 m in alpine pastures (Delforge 1995).

Orchis species grow in open to semi-shaded conditions as members of a variety of plant communities, but individual *Orchis* species vary in their tolerance to shade. *Orchis anthropophora*, for example, grows best in open habitats on grassland. In Britain it often co-occurs with tall grass species (Summerhayes 1951), *Polygala* species (Polygalaceae), and orchids including *Gymnadenia conopsea* and *Anacamptis pyramidalis* (Lang 1989) as a component of various calcicolous grasslands classed as CG3 and CG5 in the National Vegetation Classification (Rodwell 1993). However, *Orchis anthropophora* may also sometimes be found growing in the shelter of isolated bushes, among open shrubby vegetation (Summerhayes 1951), and in Mediterranean garrigue, olive groves, and woodland maquis (Davies *et al.* 1988; Delforge 1995). Similarly, *O. simia* tends to grow at its northern European sites in rough grassland habitat where it receives partial shade and shelter from the wind by nearby shrubs and trees (Summerhayes 1951; Willems and Bik 1991). Lang (1989) lists *Gymnadenia conopsea*, *Himantoglossum hircinum*, *Orchis anthropophora*, and *Anacamptis pyramidalis* as commonly co-occurring orchids. *Orchis militaris* grows in full sunlight in chalk grassland but also often in moderate shade in woodland gaps or at their margins (Summerhayes 1951; Farrell 1985; Waite and Farrell 1998). Long-term observations of *O. militaris* populations in Buckinghamshire and Suffolk indicated that this orchid declines rapidly if habitats become too heavily shaded (Hutchings *et al.* 1998). Farrell (1985) listed the principal co-occurring plants at several *O. militaris* sites in Britain and continental Europe, which include grass species in genera such as *Brachypodium*, *Briza*, *Bromus*, *Festuca*, and *Agrostis.*

Other members of the genus occur more frequently in semi-shaded conditions in woodland. For example, *O. mascula* often grows under coppiced shrubs in southern England (Summerhayes 1951) where associated species include the orchids *Listera cordata* (L.) R.Br., *Platanthera chlorantha* and *P. bifolia*, *Orchis purpurea*, and *Dactylorhiza fuchsii* (Lang 1989). Flowering can be enhanced following the periodic cutting of the shrubs when light levels increase but depressed if the shade becomes too intense such that the orchid only persists as a vegetative plant (Summerhayes 1951). In the hazel glades habitat on Öland, *O. mascula* frequently co-occurs with a number of plants such as *Anthyllis* (Fabaceae), *Pulsatilla* (Ranunculaceae), *Fragaria* (Rosaceae), *Ranunculus* (Ranunculaceae), *Geum* (Rosaceae), and *Primula* (Primulaceae) and with an even more diverse ground flora in the open alvar meadow (Nilsson 1983*a*). *Orchis purpurea* is the most shade-tolerant species of the genus. Its typical habitats in Britain at least are chalk scrub or coppice and beechwoods on the chalk escarpment in southern England (Rose 1948) where it grows in moderately deep shade. It is commonly associated with *Mercuralis*, *Helleborus*, *Daphne*, *Iris*, and *Primula*, and co-occurs with orchids such as *Cephalanthera damasonium* (Mill.) Druce, *Listera ovata*, *Ophrys insectifera*, *Orchis mascula*, *Platanthera chlorantha*, and *Dactylorhiza fuchsii* (Summerhayes 1951); it is a component of W12 woodland in the National Vegetation Classification (Rodwell 1992). It grows in filtered sunlight and conditions of high humidity and rarely in open habitats such as chalk downland in Britain, although usually in the shade and shelter of taller shrubs (Summerhayes 1951; Rose 1948).

Orchis flowers for several weeks between March and July, the exact flowering period of a population depending on the species, its geographical location, and climatic variations (Davies *et al.* 1988; Delforge 1995). One of the earliest species to flower in Britain is the early purple orchid, *O. mascula*, which can start to flower in April, but in Scotland it flowers from late April at sheltered coastal sites and in July on grassy ledges in the uplands (Allan *et al.* 1993). According to Lang (1989), *O. purpurea* normally flowers in England from mid-May to early June, but flowering is advanced to the end of April in exceptionally warm years. *Orchis* species growing in the Mediterranean region tend to bloom earlier than members of the genus in northern Europe. Willems and Ellers (1996) noted the delay in flowering time of *O. simia* with increased latitude. Populations on Cyprus flowered in April, five to six weeks earlier than comparable populations in the Netherlands, which flowered in late May. The proportion of *Orchis* plants in a population that flower varies from year to year. For example, an average of 41.1% of *O. anthropophora* plants in one study population in England flowered over a 14-year period, but the annual percentage flowering varied widely from 31.1%–72.7% (Wells 1981). Similar annual variations in the frequency of flowering of an *O. mascula* population in Sweden (Inghe and Tamm 1981; Tamm 1991) were tentatively attributed to fluctuations in climatic variables (temperature and precipitation levels in previous years), but factors controlling flowering in the genus may be more complex than this, perhaps involving, for example, activity of the fungal symbiont (Wells 1981). Periods of flowering in *Orchis* species are also interspersed with periods of dormancy. In a population of *O. militaris* in England, plants remained below ground from one to more than six years before re-emerging (Waite and Farrell 1998), whereas there was a tendency for flowering specimens of *O. mascula* in Sweden to remain vegetative the following year (Inghe and Tamm 1981; Tamm 1991). The opportunity for flowering and fruit-set may be relatively infrequent, especially given the suggestion that *Orchis* have comparatively shorter life spans than other terrestrial orchids. Half-lives of between 4.0 and 7.8 years have been estimated for *O. anthropophora* (Wells 1981) and of between 2.2 and 7.8 years for *O. militaris* (Waite and Farrell 1998), although individual plants may live longer. The oldest plants in the *O. militaris* population studied by Waite and Farrell (1998) were at least 18 years old.

Fruit production in *Orchis* species is normally low, with average fruit-set figures of about 14% for *O. italica* in Portugal, *O. mascula* in Sweden and Germany, and *O. militaris* in Germany and England (Neiland and Wilcock 1998). An even lower fruit production level of 7.8% was recorded in 1992 for *O. purpurea* in southern England (Neiland 1994); Darwin (1888) commented on the poor fruit-set of this species 100 years earlier from the same area. Seed capsules of *O. militaris* and other members of the genus take about two months to reach maturity after pollination (Farrell 1985). Germination is inferred to take place in the late summer or autumn, because seedlings of *Orchis* have been found in the field at this time (Rasmussen 1995). The plants exist as protocorms for over a year before the first tubers are formed in the second or third summer. The tubers develop into short rhizomes with mycotrophic roots in the autumn, and the first leafy shoots emerge in the following spring (Fuchs and Ziegenspeck 1927, cited in Rasmussen 1995). The roots may be heavily infected with different fungal strains. One strain was isolated from a root of *O. anthropophora* and identified as a *Rhizoctonia* species (Rasmussen 1995). Symbiotic germination of both *O. mascula* and *O. anthropophora* has been achieved with species of *Epulorhiza* (Rasmussen 1995).

Within some *Orchis* populations, many plants may flower in their first year above ground (Waite and Farrell 1998), but within others an additional two to five years may elapse before the first inflorescence develops (Wells 1981). Plants with aerial shoots, flowering or not, overwinter as a small rosette of green leaves ('winter-green' species), and the tuber is replaced annually. For example, the new tuber of *O. anthropophora* begins to develop in January and reaches full size by mid-summer when the orchid is in flower, at which time the old tuber is dying (Wells 1981). Some vegetative propagation may also be achieved if more than one tuber develops per plant, which can explain the occurrence of dense clumps of plants sometimes seen in *Orchis* populations (Waite and Farrell 1998).

Apart from *O. mascula*, which is one of the most common orchid species in Europe, and *O. anthropophora*, which is at least common in the centre and west of its distribution, many members of the genus have localized distributions and are rare. Some are endemic species; others are more widespread but rare in at least parts of their geographic range. *Orchis militaris* occurs in large populations in Russia, Germany, and Sweden but is a British Red Data Book species and categorized as 'vulnerable' because there are so few populations in southern England (Waite and Farrell 1998). Populations of *Orchis* may comprise hundreds or thousand of plants, or fewer than 50 individuals. For example, one population of *O. anthropophora* at Tottenhoe Hills in England varied between 100 and 1000 plants (Wells 1981), but one of the most well-established populations of *O. militaris* was reduced to just 43 plants prior to conservation intervention (Hutchings *et al.* 1998). Populations of such rare species are often protected but require careful habitat management to ensure their survival. Introduction of management regimes (such as removing invasive competitors and shading trees or increasing seed output by changes in the grazing regime) at populations of some rare *Orchis* species in England have proved successful in raising the recruitment rate of new plants and therefore increasing population sizes and turnover. Intensive management of one population of *O. militaris* in Buckinghamshire has altered the age structure of the population such that there has been an increase in younger plants (Hutchings *et al.* 1998), and management of another *O. militaris* population has more than doubled the apparent number of plants present at the site. **(RN)**

Pollination

The genus *Orchis s.str.* contains a number of orchid taxa that differ strongly in floral traits. *Orchis anthropophora* and *O. italica* have either no spur or only a short spur, respectively, whereas *O. mascula* and especially *O. anatolica* have long, erect spurs. No detailed studies on the pollination of *O. anthropophora* are available, and it is not clear whether nectar is secreted at the base of the labellum. The floral morphology may suggest that *O. anthropophora* is autogamous (van der Cingel 1995). It is surprising to note that for many species of this group no reliable data on their pollination biology are available. Even for widely distributed species such as *O. anatolica*, *O. quadripunctata*, *O. simia*, and *O. italica*, pollinator observations are sorely lacking. The best-studied species are *O. mascula*, *O. militaris*, and *O. galilaea* Schltr. *Orchis mascula* is mainly pollinated by *Bombus* queens and *Psithyrus* females (Nilsson 1983*a*). *Orchis militaris* on the other hand is adapted to short-tongued pollinators such as members of the Andrenidae and Halictidae. Long-tongued flower visitors such as honey bees (*Apis mellifera*) or bumble-bees (*Bombus* spp.) do not pick up the pollinaria because they reach the end of the spur before touching the viscidium (Vöth 1987). In contrast to these species, *O. galilaea* does not exploit food-searching insects but sexually deceives males of the solitary bee *Halictus marginatus* (Bino *et al.* 1982). Apart from *O. galilaea*, pollination by sexual deceit in Orchidinae has only been reported in the genus *Ophrys*. **(AW, SC, AD)**

Uses

The tubers of several orchids in Europe and the Middle East, particularly of *O. mascula* and certain other species of *Orchis*, contain a highly nutritious starch-like substance known as 'bassorin', that can be extracted by drying and subsequent powdering. Collection of tubers for this purpose has long been practised both in Europe and Asia. The product is now generally known as 'salep' or even 'saloop', both English corruptions of the Arabic name *sahlab*, which was itself thought by Forsskal and others to have been a corruption of the

Arabic name *tha'lab*, a fox. Täckholm & Drar (1969) explained that, although salep was then only to be found in powdered form in the markets of Cairo, it was in former times exhibited there and sold as strings of the dried orchid tubers under such names as *khusa al-kalb* or *khusa ath-tha'lab* ('dog's testicles' or 'fox's testicles'), which the rather shrivelled, blackened tubers appeared to resemble. The former of these two common names is mentioned by Ibn al-Baitar (*c.* 1240). Composed of approximately 27% starch and 48% mucilage, it produces a highly nourishing and easily digested demulcent food when mixed with about 50 parts of water. This beverage (known as *sahlab*) has since ancient times been given to children; also, when flavoured and mixed with milk, sugar, chopped nuts, etc. and warmed, it provided a drink for adults that was particularly popular during the cold season of the year. There appears to be little solid basis for claims that it was also an aphrodisiac, although these are referred to by Ibn al-Baitar. Salep is also used as an ingredient in the manufacture of ice cream in Turkey and parts of the Middle East. **(JW)**

Cultivation

Some species will naturalize easily (e.g. *O. mascula*, *O. laxiflora*). Most grow well in alpine house conditions, using compost C with added lime for those from calcareous areas. **(CB)**

Taxonomic notes

Orchis has long been regarded as a heterogeneous genus. Recently, however, Delforge (1995) defined several discrete groups within it. Results from molecular studies (Pridgeon *et al.* 1997; Bateman *et al.* 1997) confirmed this view, leading to the transfer of *O. morio* and relatives to the genus *Anacamptis* and the transfer of *O. tridentata* and relatives to *Neotinea*, leaving *Orchis s.s.* typified by *O. militaris.* Molecular and morphological evidence (Pridgeon *et al.* 1997; Bateman *et al.* 1997) supports the inclusion of *Aceras* in *Orchis s.s.* **(JW)**

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90. PECTEILIS

Pecteilis Raf., *Fl. Tellur.*, **2**, 37 (1836); Seidenfaden, *Dansk Bot. Arkiv.*, **31** (3), 22 (1977). Type species: *P. susannae* (Bl.) Raf.

Hemihabenaria Finet, *Rev. Gen. Bot.*, **13**, 506 (1901). Type species not designated.

Parhabenaria Gagnep., *Bull. Mus. Hist. Nat. Paris*, ser.2, **4**, 597 (1932). Type species: *P. cambodiana* Gagnep.

Derivation of name

From the Greek *pectein*, a comb, describing the lacerate side lobes of the lip of the type species. **(PC)**

Description (Plate 109; Fig. 90.1)

Medium-sized to large terrestrial *herbs* with large tubers. *Stem* erect, stout, leafy. *Leaves* cauline or in a basal three-rosette, several, ovate-elliptic or ovate, rather fleshy, green. *Inflorescence* sparsely to densely flowered. *Flowers* medium sized to large, showy, white, or white with a yellow lip, arranged in a spiral. *Sepals* and *petals* entire; the petals linear, much smaller than the sepals; sepals elliptic, connivent to form a hood over the column. *Labellum* decurved, more or less three-lobed, spurred at base, lacking a callus; side lobes spreading, often fringed-lacerate, rarely entire; mid-lobe smaller, entire; spur pendent, serpentine, straight or U-shaped, cylindrical, elongate. *Column* erect; anther loculi widely spaced on a broad connective, sometimes coherent above; pollinia two, clavate, sectile; viscidia two, ovate to oblong, concealed; lateral appendages present, sessile; rostellum three-lobed, side lobes tapering, often slightly incurved at apex; mid-lobe erect, blunt; stigmas sessile, adherent to base of lip. *Ovary* shortly pedicellate. **(PC)**

Distribution (Fig. 90.2)

A genus of about eight species in southern and eastern Asia and the Malay Archipelago. **(PC)**

Cytogenetics

Two species of *Pecteilis*, *P. radiata* Raf. and *P. latilabris* (Lindl.) Mitra, have a complement of x = 16 with diploid $2n = 2x = 32$ and polyploid $2n = 3x = 48$, $2n = 4x = 64$ for the former and x = 21 with diploid $2n = 2x = 42$ for the latter (Miduno 1939, 1940; Arora 1971). **(SD)**

Ecology

Pecteilis species grow in grassland habitats at high elevations, for example *P. susannae* Raf. at 1000–2000 m and *P. triflora* (D. Don) T. Tang & F. T. Wang at 400–1200 m in the Himalayas (Hara *et al.*

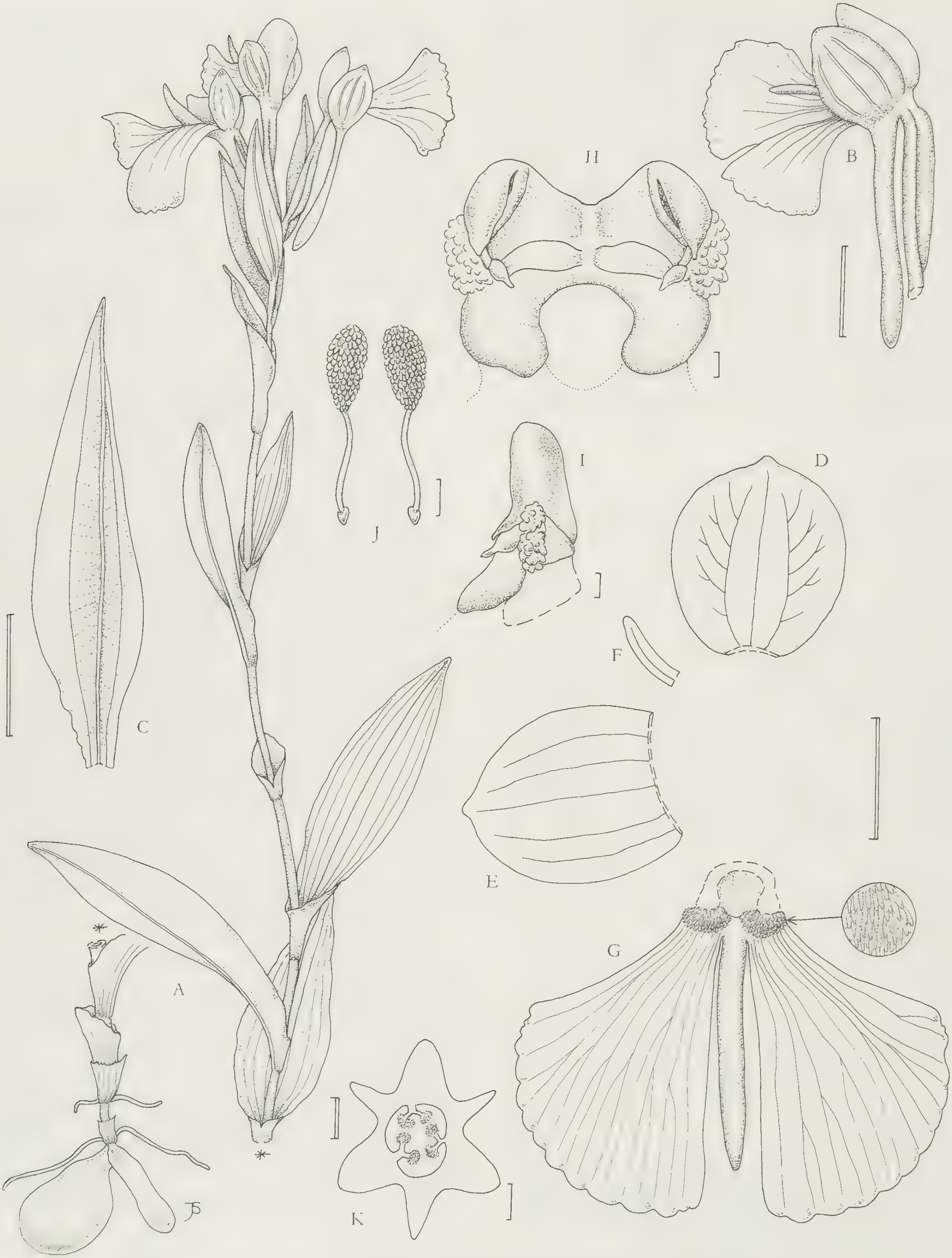

Fig. 90.1. *Pecteilis triflora* (D. Don) T. Tang & F. T. Wang. A. Habit; B. Flower, side view; C. Bract; D. Dorsal sepal; E. Lateral sepal; F. Petal; G. Labellum; H. Column, front view; I. Column, side view; J. Pollinaria; K. Ovary, transection. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Williams & Stanton 8301* and Kew Spirit Collection no. 17310.

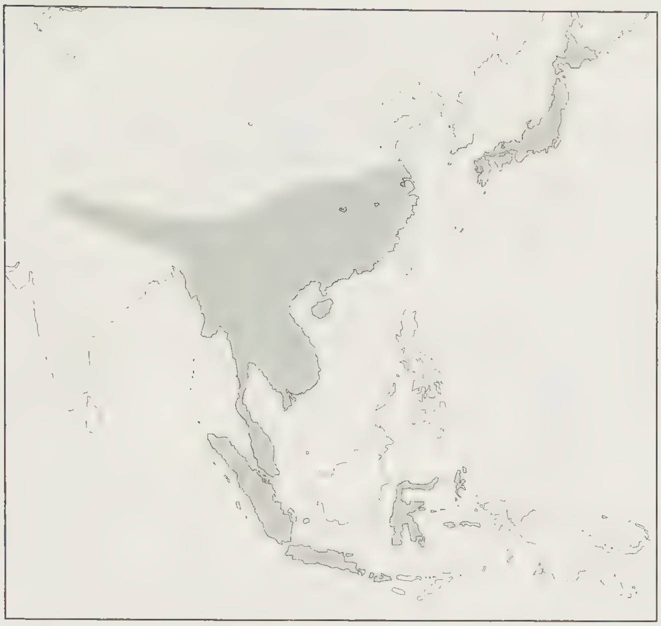

Fig. 90.2. Distribution map of *Pecteilis.*

1978; Polunin and Stainton 1984). *Pecteilis radiata* Raf. from Korea and Japan flowers in the summer (Cullen 1992), and the more widespread *P. susannae* flowers in August to September throughout its range (Polunin and Stainton 1984). *Pecteilis* is widely dispersed throughout its range. In China it occurs in Jiangsi, Guangxi, Guangdong, Guizhou, Sichuan, Yunnan, and the South China Sea islands (Chen and Tang 1982). **(RN)**

Uses

Pecteilis susannae is a showy orchid and occasionally is seen in cultivation. The tubers are eaten by forest tribes and by wild pigs in India where they are also used as a cure for bleps or bullae, especially on the palm of the hand (Chopra *et al.* 1969). **(PC)**

Cultivation

Showy mountain plants with a history of cultivation (*P. susannae*). Compost B and D. **(CB)**

Taxonomic notes

Pecteilis was established by Rafinesque and later recognized by Finet (as *Hemihabenaria*; 1901) and Schlechter (1919). It is distinguished from *Habenaria*, into which some authors have lumped it, by its column structure, which is somewhat similar to those of *Habenaria* and *Gymnadenia.* In particular, the anther loculi are widely spaced on the connective, and the stigmas are sessile and adnate to the base of the lip. **(PC)**

Taxonomic literature

Seidenfaden, G. (1977). *Pecteilis. Dansk Botanisk Arkiv*, **31,** 22.

91. PERISTYLUS

Peristylus Blume, *Bijdragen*, 404 (1825). Type species: *P. grandis* Blume (lectotype selected by Seidenfaden, 1977).

Glossula Lindl., *Bot. Reg.*, **10**, ad t. 862 (1825). Type species: *G. tentaculata* Lindl.

Habenaria sect. *Peristylus* (Blume) Benth. in Benth. & Hook.f., *Gen. Pl.*, **3**, 625 (1883), *orth. var.*

Derivation of name

From the Greek *peri*, around, and *stylos*, a column, in allusion to the prominent column arms on each side of the column. **(PC)**

Description (Plate 110; Fig. 91.1)

Small to medium-sized terrestrial *plants* with small oblong to ellipsoid tubers. *Leaves* several, in a basal rosette, clustered in the middle of the stem or spirally arranged along stem, ovate to lanceolate or oblanceolate, sheathing at the base, thin-textured. *Inflorescence* terminal, sparsely to densely flowered; bracts lanceolate, as long as or shorter than the flowers. *Flowers* resupinate, small, spirally arranged, green or yellowish green, perianth persistent in fruit. *Dorsal sepal* and *petals* entire, free, connivent or slightly spreading, lateral sepals oblique. *Labellum* connate at base with margins of column, distally three-lobed or entire, larger than the sepals and petals, often clawed at the base, spurred at the base, ecallose or with a fleshy callus in front of the mouth of the spur; spur scrotiform to cylindric, shorter than to longer than the labellum, usually shorter than the ovary. *Column* short, conical, erect; anther bilocular, with adjacent loculi; lateral appendages sessile; pollinia two, shortly clavate, sectile; viscidia two, ovate to oblong; rostellum small, trilobed but with lateral lobes short and mid-lobe smaller than anther loculi; stigmatic arms two, remote, sessile, convex or depressed centrally, adnate to base of lip and lateral appendages. *Ovary* almost lacking a pedicel. **(PC)**

Distribution (Fig. 91.2)

A genus of 70–75 species in eastern Asia, south-eastern Asia, the Malay Archipelago, north-eastern Australia, the Philippines, and south-western Pacific islands. **(PC)**

Infrageneric treatment (PC)

Seidenfaden (1977) tentatively suggested a division into four sections based on floral morphology as follows:

Flowers with a bipartite lip divided into a hypochile and tripartite epichile based upon *P. gracilis* Blume;

Flowers with an ecallose lip lacking a bipartite nature and trilobed in the middle;

Flowers with a callus on the disc of the lip;

Flowers with a simple rather than a tripartite lip

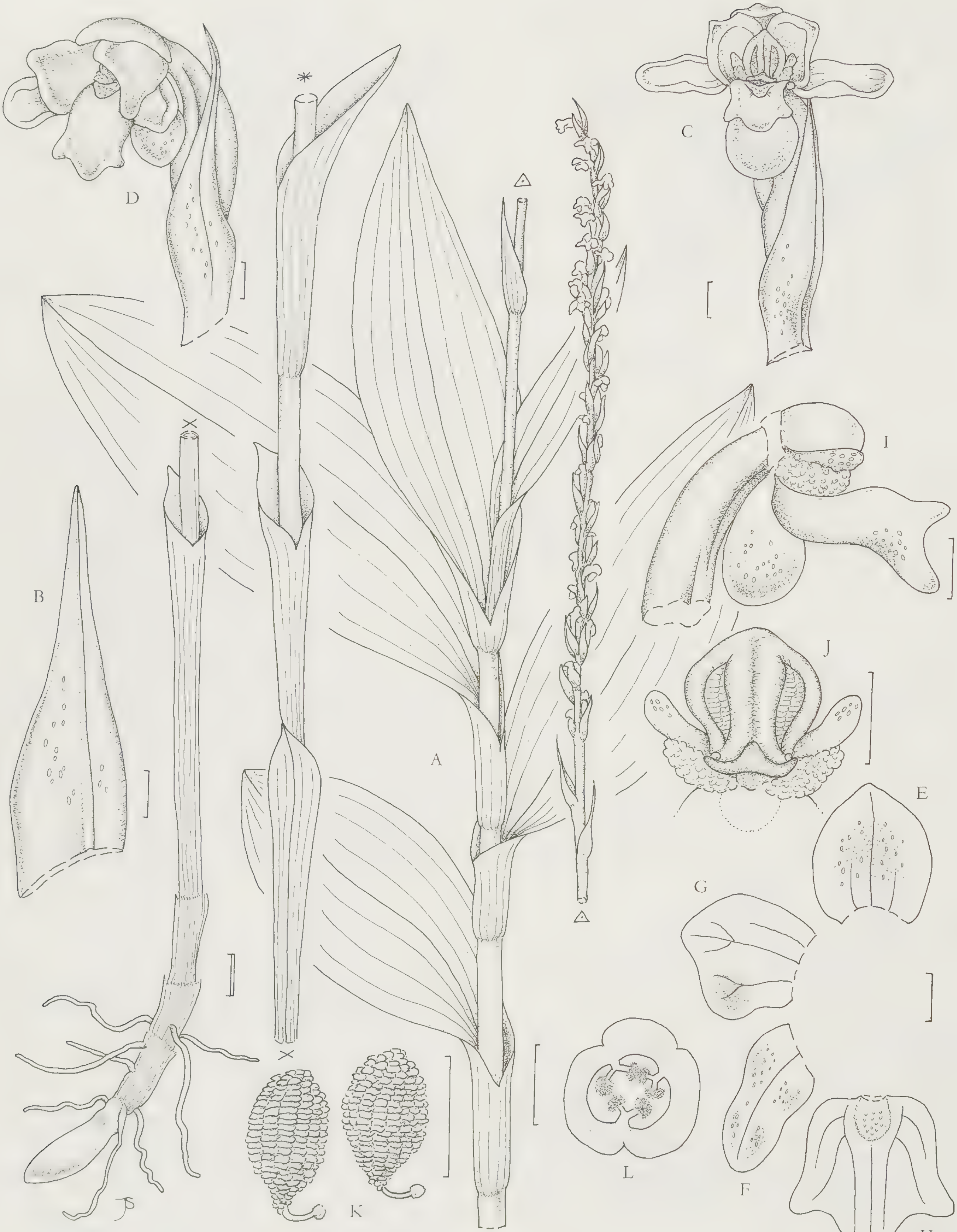

Fig. 91.1. *Peristylus goodyeroides* Lindl. A. Habit; B. Bract; C. Flower, front view; D. Flower, oblique view; E. Dorsal sepal; F. Lateral sepal; G. Petal; H. Labellum; I. Labellum and column, side view; J. Column, front view; K. Pollinaria; L. Ovary, transection. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Barnes H-39/1944* and *Lace 5297* and from Kew Spirit Collection no. 19414.

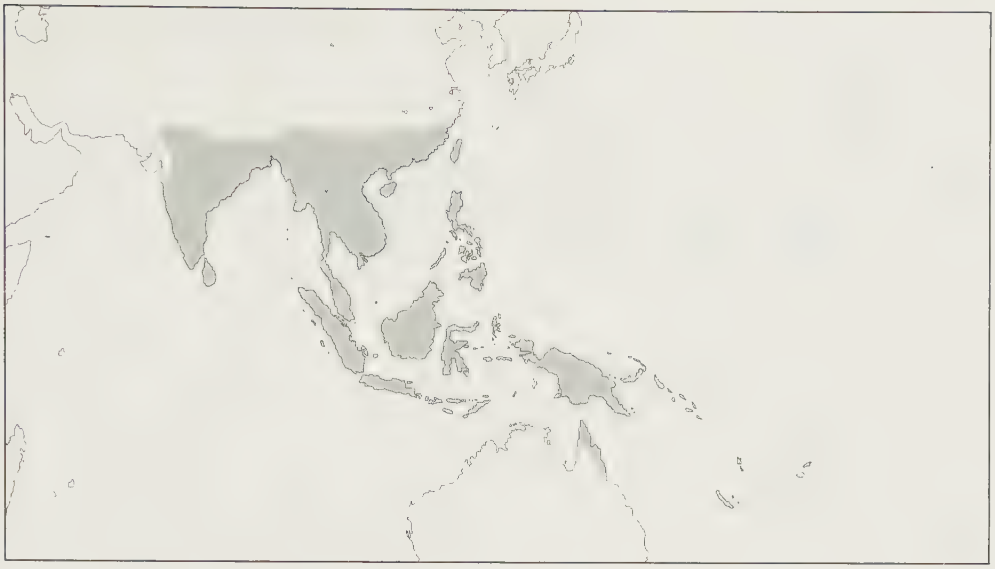

Fig. 91.2. Distribution map of *Peristylus*.

Cytogenetics

The genus *Peristylus* has two basic numbers, x = 21 and x = 23 (Table C.2), although x = 21 is more reliable. The presence of a diploid number of $2n = 28$ indicates an ancestral basic number of x = 7. **(SD)**

Phytochemistry

Glucomannans have been detected in the tubers of *P. viridis* Lindl. (Ohtsuki 1937). This study was carried out as part of a survey of the constituents of the tubers of a number of Japanese orchid species. **(NV, RG)**

Ecology

Peristylus species grow in Nepal and southern China at 2000–2500 m. *Peristylus fallax* Lindl. occurs between 2700 and 3700 m from Garhwal to Sikkim in the Himalayas. Other members of the genus occur at lower levels; *P. lawii* Wight grows in Nepal and India at 400–1000 m (Hara *et al.* 1978). Some *Peristylus* species grow in habitats with full sunlight. For example, *P. brevilobus* Thw. is found in hill cuttings in the Himalayas growing in the open with other terrestrial orchids and non-orchid herbs. Other *Peristylus* species grow under the shade of trees in montane temperate forest, subtropical montane forest, or tropical wet evergreen forests and in a moist substrate especially on the banks of streams. The flowering period of *Peristylus* varies according to species, with some flowering between September and February and others from April to August.

The genus includes some narrowly endemic species with restricted distributions, such as the rare Himalayan endemics *P. brevilobus* Thw. and *P. trimenii* (Hook.f.) Abeyw. (Dassanayake 1981), but other species are common in favourable habitats. In China *Peristylus* occurs in the following regions: Hainan and the South China Sea islands, Jiangsi, Kwangsi, Guangxi, Guangdong, Sichuan, and Yunnan (Chen and Tang 1982). Renz and Vodonaivalu (1989) noted that *Peristylus* is the dominant member of 'Habenariinae' in Melanesia, such as Fiji. **(RN)**

Uses

None recorded. **(PC)**

Cultivation

Compost C and D. **(CB)**

Taxonomic notes

The distinction of *Peristylus* from *Habenaria* has been debated at some length (e.g. Seidenfaden 1977; Kores 1989). Vegetatively they are indistinguishable, but current views support the retention of the former as a distinct genus on the basis of column structure. In particular the stigma lobes of *Habenaria* are stalked (termed stigmatophores) and free from the lip base. In *Peristylus* they are reduced to pulvinate swellings at the base of the column, which is adnate to the base of the lip. Most *Habenaria* species have larger flowers, but the range of flower size overlaps that of *Peristylus*. **(PC)**

Taxonomic literature

Seidenfaden, G. (1977). Peristylus Bl. *Dansk Botanisk Arkiv*, **31,** 27.

Kores, P. (1989). 3. *Peristylus* Bl. *Allertonia*, **5**, 11.

92. PHYSOCERAS

Physoceras Schltr., *Feddes Repert. Spec. Nov. Regni Veg. Beih.*, **33**, 78 (1924). Type species: *P. bellum* Schltr. (lectotype selected in *Index Nom. Gen.* 64/24066, 1967).

Derivation of name

From the Greek *physa*, a bladder, and *keras*, a horn, in allusion to the vesicular, often minutely apiculate, spur of the flower. **(PC)**

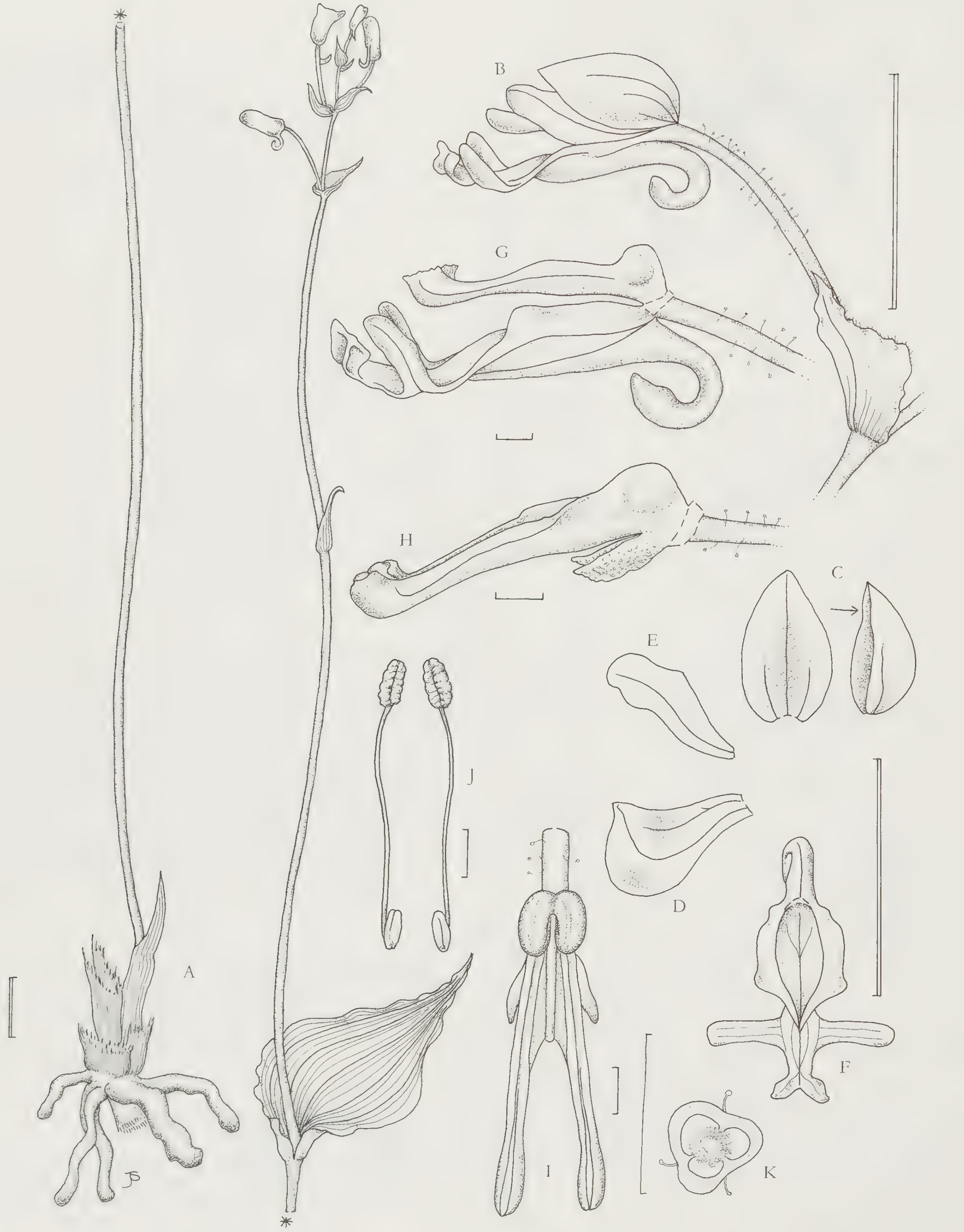

Fig. 92.1. *Physoceras bellum* Schltr. A. Habit; B. Flower, side view; C. Dorsal sepal, front and side views; D. Lateral sepal; E. Petal; F. Labellum; G. Labellum and column, side view; H. Column, side view; I. Column, front view; J. Pollinaria; K. Ovary, transection. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Humbert & Cours 22904*.

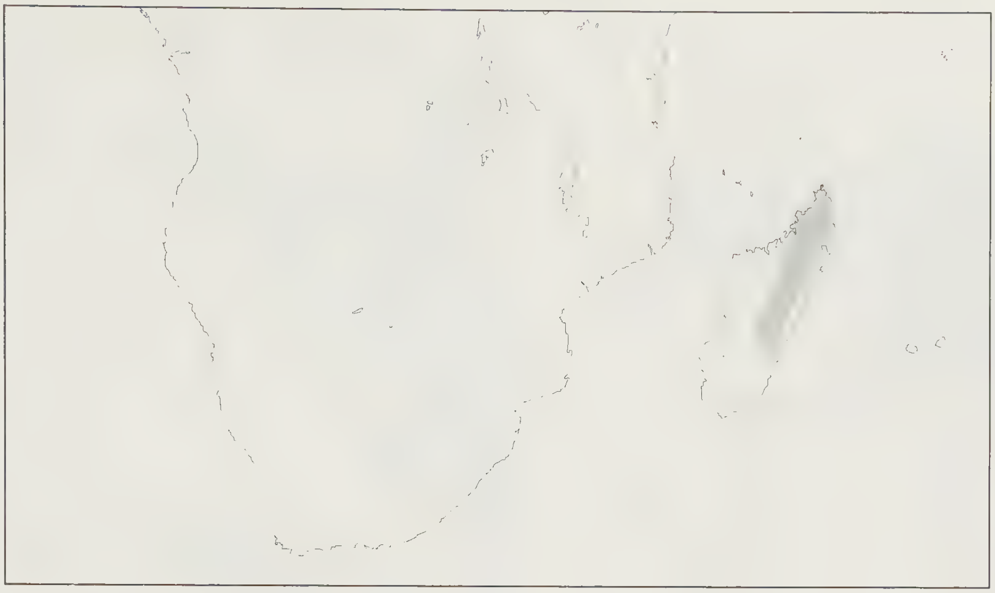

Fig. 92.2. Distribution map of *Physoceras.*

Description (Plate 111; Fig. 92.1)

Terrestrial or epiphytic, erect to spreading *herbs* with swollen fleshy roots. *Stems* 1–2, unifoliate, enclosed at the base by brown or black sheaths. *Leaf* borne in the middle of the stem, ascending, ovate-cordate, green. *Inflorescence* terminal, racemose, sparsely to densely 2–10-flowered; bracts, free lanceolate. *Flowers* often showy for size of plant but sometimes small, white, pink, lilac, or purple. *Dorsal sepal* free, hooded. *Lateral sepals* free, spreading. *Petals* smaller than dorsal sepal and adnate to it forming a hood over the column. *Labellum* three-lobed, ecallose, the mid-lobe emarginate, larger than the spreading side lobes; spur cylindrical, pendent, or incurved. *Column* erect; anther canals elongate; pollinia two, clavate, viscidia two; rostellum trilobed, side lobes elongate, each forming a bursicle at the apex; stigma bilobed. **(PC)**

Distribution (Fig. 92.2)

A small genus of five species endemic to Madagascar. **(PC)**

Ecology

The Malagasy genus *Physoceras* comprises terrestrial, epiphytic, or lithophytic orchids that grow in a variety of habitats including moss forest, lichen-rich forest, river margins, montane ericaceous scrub, and humid evergreen forests. Most species grow at elevations of 1000–2500 m, although the epiphytic species, *P. violaceum* Schltr., is reported to grow at about 500 m in humid evergreen forests (Du Puy *et al.* 1999). On the mountain summits, *Physoceras* grows with a few other cool-growing orchids such as *Angraecum*, *Cynorkis*, and *Polystachya* species among shrubs (Hillerman and Holst 1986). The flowering period of *Physoceras* is usually between October and January, although *P. bifurcum* H. Perr. flowers in March–April and *P. rotundifolium* H. Perr. and *P. violaceum* in July and August, respectively (Du Puy *et al.* 1999). **(RN)**

Uses

None recorded. **(PC)**

Cultivation

Composts C and E. **(CB)**

Taxonomic notes

The most recent account of the genus is given by Perrier de la Bâthie (1939). An updated nomenclature is provided by Du Puy *et al.* (1999). **(PC)**

Taxonomic literature

Du Puy, D., Cribb, P. J., Bosser, J., Herman, J., and Herman, C. (1999). *Orchids of Madagascar.* Royal Botanic Gardens, Kew.

Perrier de la Bâthie, H. (1939). Orchidées. In *Flore de Madagascar* I. (ed. H. Humbert). Tananarive Imprimerie Officielle, Madagascar.

93. PLATANTHERA

Platanthera Rich., *De Orch. Eur. Annot.*, **20**, 26 (1817), preprint of *Mém. Mus. Hist. Nat. Paris* **4**, **42**, 48 (1818). Type species: *Platanthera bifolia* (L.) Rich.

Tulotis Raf., *Herb. Raf.*, 71 (1833). Type species: not designated.

Blephariglottis Raf., *Fl. Tellur.*, **2**, 38 (1836). Type species: not designated.

Limnorchis Rydb., *Mem. N. Y. Bot. Gard.*, **1**, 293 (1900). Type species: not designated.

Lysiella Rydb., *Mem. N. Y. Bot. Gard.*, **1**, 104 (1900). Type species: *Lysiella obtusata* (Pursh) Rydb.

Gymnadeniopsis Rydb., in *Britton, Man. Fl. N. States & Canada*, 293 (1901). Type species: not designated.

Piperia Rydb., *Bull. Torrey Bot. Club*, **28**, 269 (1901). Type species: *Piperia elegans* (Lindl.) Rydb.

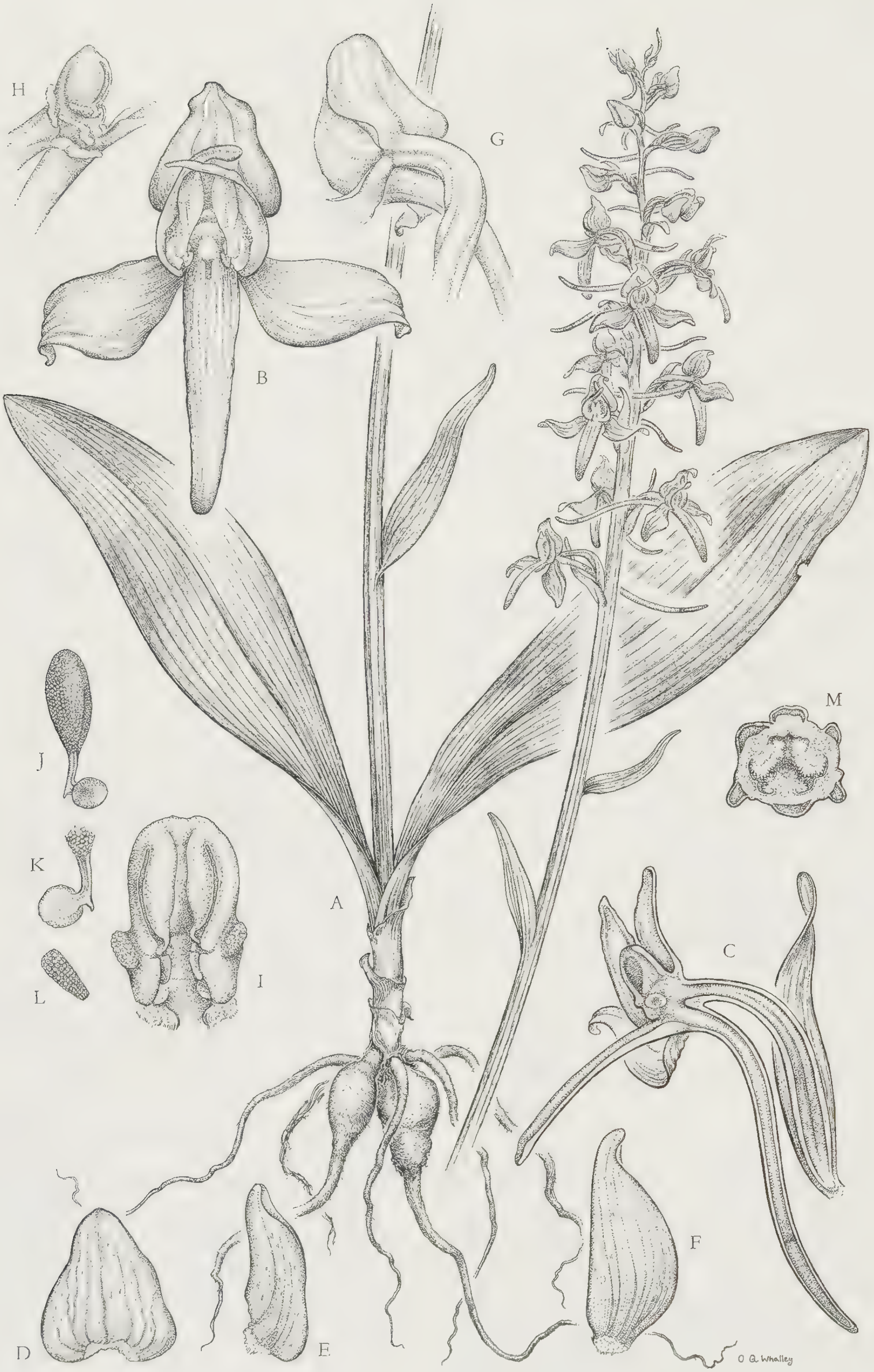

Fig. 93.1. *Platanthera bifolia* (L.) Rich. A. Habit, ×1; B. Flower from front, ×6; C. Flower, ovary, and bract (longitudinal section), ×6; D. Dorsal sepal, ×6; E. Petal, ×6; F. Lateral sepal, ×6; G. Flower from back, ×6; H. Column from side, ×6; I. Column from front, ×6; J. Pollinarium, ×9; K. Viscidium and caudicle, ×15; L. Part of pollinium, ×45; M. Ovary, transverse section, ×9. Drawn by Oliver Q. Whalley from Kew Spirit Collection nos. 34474, 22571, and 22572.

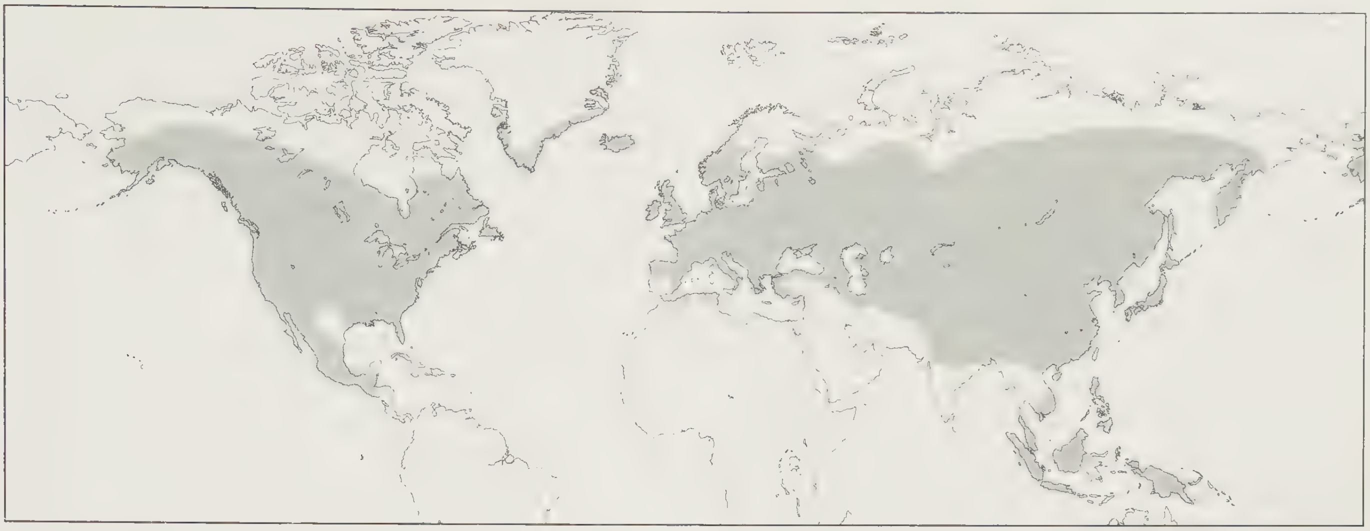

Fig. 93.2. Distribution map of *Platanthera.*

Derivation of name

From the Greek *platys*, wide, broad, and Latin *anthera*, anther, in reference to the unusually wide anther. **(JW)**

Description (Plate 112; Fig. 93.1)

Small to medium-sized *herbs. Rootstock* tuberous, or composed of a fascicle of fleshy, tapered roots, tubers (when present) entire, fusiform or ovoid. *Stem* erect, leafy or not. *Leaves* two or three at the base and/or cauline, unspotted. *Inflorescence* cylindrical, usually rather sparsely flowered (rarely many-flowered), sometimes dense; floral bracts leafy. *Flowers* medium sized or small, greenish, white, orange, yellow, or rose-pink, often sweetly scented. *Dorsal sepal* and *petals* usually connivent, forming a hood. *Lateral sepals* free or lower margins partly adnate to base of lip, spreading or recurved. *Labellum* entire and strap-shaped, divided or fimbriate to varying degrees, sometimes with a central thickening, spurred, spur varying in length, filiform or narrowly cylindrical, sometimes clavate above the middle, the orifice situated below the stigma, sometimes with a wide and deep nectary entrance created by expanded margins of the labellum base, which adhere to the sides of the column. *Column* short, rather truncate; rostellum flattened, triangular, with a rudimentary median lobe; anther broad, immobile, loculi more or less separated by connective tissue or the stigma, either divergent or convergent and parallel to varying degrees; pollinia two, clavate or each cleft into two halves, with caudicles attached to naked viscidia, bursicles absent. *Ovary* cylindrical to fusiform, curved toward apex, sessile, twisted, glabrous. **(JW)**

Distribution (Fig. 93.2)

Approximately 200 species (Luer 1975) distributed over Europe and North Africa, extending eastward across Asia to New Guinea, North and Central America. **(JW)**

Infrageneric treatment

Luer (1975) recognized five sections in *Platanthera* as follows:

Platanthera section **Blephariglottis** (Raf.) Luer contains species with a fimbriate labellum from North America.

Platanthera section **Gymnadeniopsis** (Rydb.) Luer, also from North America, have close, more or less converging anther loculi and resemble the European *Gymnadenia* in appearance.

Platanthera section **Tulotis** (Raf.) Luer, from North America and parts of northern Asia, have a labellum with a tubercle on it.

Platanthera section **Platanthera**, including the type of the genus, have the typically broad anther with divergent loculi, and one or two basal leaves.

Platanthera section **Limnorchis** (Rydb.) Luer, with an entire labellum and more or less divergent loculi, contains the taxonomically critical *P. dilatata*/*P. hyperborea* complex, distributed primarily in North America.

At various times each of these has been recognized by some authors at generic rank, but further work is needed to choose definitively among these options. **(JW)**

Palynology

Three species of *Platanthera* (*P. bifolia, P. chlorantha, P. hyperborea*) were examined by Schill and Pfeiffer (1977), and all have laevigate sculpturing. **(AP)**

Cytogenetics

In the genus *Platanthera* the basic number is x = 21 (Cauwet-Marc and Balayer 1986; Yokota 1987; Dalgaard 1989). The chromosomes are larger than those of many species of *Neotinea*, *Orchis*, *Dactylorhiza*, or *Gymnadenia*. *Platanthera chlorantha* has a symmetrical karyotype. Giemsa C-banding in two species of *Platanthera* revealed small and medium-large centromeric heterochromatin. **(SD)**

Phytochemistry

The phenolic glucoside loroglossin was isolated from *P. bifolia* (Delauney 1921*c*) and its structure later determined to be *bis* [4-(β-D-glucopyranosyloxy) benzyl] *erythro*isobutyltartrate by Aasen *et al.* (1975; Fig. 81.4). Ohtsuki (1937) analysed the glucomannans of the tubers of many Japanese orchid species, including *P. florentii* and *P. ophrydioides* F. Schmidt.

Investigation of the flavonoid content of the leaves of *P. bifolia* and *P. hyperborea* (L.) Lindl. revealed the presence of both the flavonol quercetin and flavone *C*-glycosides. In addition, the leaves of *P. bifolia* contain the flavonol kaempferol. The flavonol aglycones were detected in acid-hydrolysed extracts of leaf tissue, indicating that they originate from flavonol *O*-glycosides (C. A. Williams 1979).

The chemical compositions of the scents of *P. bifolia* and *P. chlorantha* flowers were obtained by gas chromatography coupled with mass spectroscopy (Tollsten and Bergström 1989; Kaiser 1993). The principal components of the scent of *P. bifolia* flowers are esters (methyl benzoate and methyl salicylate) and monoterpenes (linalool and (*E*)-ocimene) according to Kaiser (1993). However, many other compounds present as minor components are thought to give the scent its characteristic fragrance, notably the so-called 'lilac aldehydes' (Wakayama *et al.* 1973; Wakayama and Namba 1974). Considerable variation was found in the scent composition of different populations of *P. bifolia* (Nilsson 1985; Tollsten and Bergström 1993). The scent of *P. chlorantha* flowers (which like that of *P. bifolia* is emitted during the night) consists principally of methyl benzoate, linalool, and geraniol but can also vary among different populations. A detailed analysis of the floral fragrance of *P. stricta* was presented by Patt *et al.* (1988). **(NV, RG)**

Ecology

The terrestrial genus *Platanthera* usually grows on damp and acidic soils, although sometimes it occurs on drier and/or calcareous substrates. *Platanthera hyperborea* is reported to grow in permanently wet and acidic soils of swamps and marshes across its range in the USA (Hitchcock *et al.* 1969), Europe, and Asia (Hultén 1927; Delforge 1995). However, it occasionally grows on dry grassland, as in the high mountain regions of Japan (Ohwi 1965; Delforge 1995) and according to Hitchcock *et al.* (1969) occurs in the Pacific Northwest of the US in bogs where the soil can be of calcareous origin. Other *Platanthera* species tolerant of a range of different soil types include *P. bifolia*, which usually grows on damp acidic or neutral substrates, as in the heaths and moorlands of Scotland, but occurs less frequently on calcareous soils such as the chalk downs of southern England (Summerhayes 1951; Allan *et al.* 1993). Likewise, in Finland *P. bifolia* plants have been reported to grow in both the dry and open habitats of the archipelagos and coastal areas and in the wetter and shadier habitats of woodland and forests (Haeggstrom 1994). The closely related *P. chlorantha* differs markedly in its ecological preferences. It typically grows on calcareous and alkaline soils and in warmer and drier conditions than *P. bifolia* and is consequently more abundant in southern England. However, it also grows in a variety of other habitats such as more acidic heathlands (Summerhayes 1951), and sometimes the two species can be found growing together in the same habitat (Summerhayes 1951; Nilsson 1983*b*).

Platanthera grows in a variety of habitat types including marshes on taiga and tundra, moors and heaths, sphagnum and peat bogs, swamps, shrubland, open deciduous woodlands and coniferous forests. Consequently *Platanthera* species are subject to varying light conditions, from full sun to dense shade. Some commonly occur in open habitats but can tolerate lower light levels. For example, *P. bifolia* in Britain is a common plant of heaths and moorlands, growing among such species as heather (*Calluna vulgaris* Salisb.), cross-leaved heath (*Erica tetralix* L.), and mat grass (*Nardus stricta* L.). It also occurs in bogs with sedges (*Carex* species), sweet gale (*Myrica gale* L.), and the common marsh orchid (*Dactylorhiza praetermissa*) and in upland meadows and fields with other orchids including *D. fuchsii*, *D. maculata* ssp. *ericetorum*, *Gymnadenia conopsea*, and *P. chlorantha*. In all of these habitats, *P. bifolia* receives comparatively high light levels, but it can also grow in shaded environments, such as beechwoods in southern England where it occurs with *Listera ovata* and other woodland orchids (Summerhayes 1951; Allan *et al.* 1993). *Platanthera chlorantha* is a more typical woodland species (Davies *et al.* 1988). Summerhayes (1951) noted that it is characteristic of coppiced oak woods of southern England where it occurs with *Orchis mascula*, *L. ovata*, and *D. fuchsii*, whereas in Suffolk it occurs in a number of ancient woods growing on chalky boulder clay (Sanford 1991). Elsewhere in England, it is found in scrubland where it is shaded by bushes and small trees and often co-occurs with *Cephalanthera damasonium* and *O. insectifera* when on chalk (Summerhayes 1951). In Scotland its most usual habitat is open pasture and grassland (Allan *et al.* 1993). By comparison, in the United States many *Platanthera* species grow in deep sphagnum and mud in forest areas comprising conifers such as tamaracks, cedars, balsams, and firs (Luer 1975). *Platanthera orbiculata* (Pursh) Lindl. is widespread in the forests of North America including coniferous swamps, and *P. macrophylla* (Goldie) P. M. Brown is found in mesic areas of the eastern mixed forest (Reddoch and Reddoch 1993). *Platanthera hyperborea* is said to tolerate deep shade in its woodland habitats (Hitchcock *et al.* 1969), although *P. grandiflora* (Bigelow) Lindl. occurs in full sun to shade in the Appalachian Mountains, frequently under or near conifers (Stoutamire 1974). Flowering of some *Platanthera* species growing in woodlands can be suppressed by dense shade. Both *P. bifolia* and *P. chlorantha*, for example, tend to be distributed in gaps in woodlands, and their frequency of flowering is increased following coppicing or felling of trees (Summerhayes 1951; Sanford 1991).

Platanthera species grow at a range of elevations from lowlands to mountain regions. The North American species *P. grandiflora* exemplifies the range that can be achieved by some individual species. In the north of the United States, *P. grandiflora* grows at sea level in the New England states, but farther south it is restricted to the high elevations of the Appalachian uplands (Stoutamire 1974). Similarly, the widespread *P. hyperborea* occurs both in low-lying marshes and bogs (Hultén 1927) and dry alpine grassland up to 3000 m, although it is far less common at high elevations (Delforge 1995; Ohwi 1965). In Britain, *P. chlorantha* is more lowland in distribution than *P. bifolia* (Summerhayes 1951).

Flowering of *Platanthera* normally takes place between late May and early August (Davies *et al.* 1988), the exact period varying among species and influenced by factors such as microclimate and the elevation and latitude of individual populations. In Britain *P. chlorantha* usually flowers in June to July, but in an early season or in sheltered localities it may start to flower in May (Summerhayes 1951). Also, *P. chlorantha* usually commences flowering 2–3 weeks before *P. bifolia* (Delforge 1995). During the flowering period, the leaves of *Platanthera* species remain green ('summer-green' orchids), but they senesce in the autumn, and the plants overwinter as underground tubers.

The number of flowering plants in *Platanthera* populations fluctuates from year to year, a feature that has been attributed to seasonal climatic variations. During their 10-year study of a *P. chlorantha* population in southern Scotland Dickson and Parkes (1994) observed that fewer plants flowered following years when rainfall levels between April and August were particularly low and that there was premature floral senescence of flowering plants during dry summer months. According to Summerhayes (1951), a large proportion of plants in many *P. chlorantha* populations in England do not flower in most years, although they may persist in a vegetative form for a long period until conditions are more favourable for flowering stems to be produced. Aerial stems in *Platanthera* develop in springtime from overwintered buds formed in the preceding growing season and utilize food stored in the tuber also produced that year. Usually a new bud and tuber develop each year as replacements. They form at the base of the aerial stem during the latter half of the growing season, the tuber is already well developed by the time the flowers open (Summerhayes 1951). Sheviak (1990) noted for *Platanthera* species, including *P. hyperborea*, that if the bud or shoot is accidently destroyed or damaged by late frost, foraging animals, disease, or inappropriate management practices, the orchid is unable to recover and usually dies. He contrasted this feature of *Platanthera* to that of other orchids including *Cypripedium* species, in which similar damage may simply result in suppression of flowering capacity for two or more years. Since normally only one new bud and tuber are formed per year per plant, and since *Platanthera* species have no other means of vegetative propagation, increase in population size by vegetative growth rarely occurs (Summerhayes 1951). One exception is *P. obtusata*, an arctic/subarctic species, which commonly develops more than one tuber each season. This must be of adaptive advantage in an environment in which the short flowering season could make seed production very irregular (Hesselman 1900, cited in Rasmussen 1995). Most other *Platanthera* species, however, are likely to be entirely dependent on seed dispersal for increasing population size and colonization of new habitats.

Fruit production in *Platanthera* species is often high with average fruit-set figures of between 50% and 60% recorded for *P. ciliaris* Lindl. and *P. stricta* Lindl. in the USA and *P. chlorantha* in Sweden and 90% for *P. mandarinorum* Rchb.f. subsp. *hachijoensis* (Honda) Hiroe in Japan (Neiland and Wilcock 1998). Reports of lower fruit-set levels are unusual, for example less than 30% in two *Platanthera* species from Japan (Inoue 1985, 1986). For the rare North American species *P. integrilabia* (Correll) Luer, the low fruit-set of 13.6% in one population may be explained by low levels of self-pollination in the absence of pollinating insects (Zettler and Fairey 1990). A higher fruit-set of 56.9% was achieved in a large population of this rare orchid in Tennessee where pollinators were seen to be present (Zettler *et al.* 1996). Plants in this population produced a mean of 4.7 capsules per inflorescence. With each capsule containing 3433 seeds, the average seed output per plant was estimated to be *c.* 16 000 (Zettler *et al.* 1996). Salisbury (1942) counted 2500 seeds in one capsule of *P. chlorantha* and calculated that the average output of seeds per plant could be 13 750 for a population in England. A count of the ovule number per ovary in a *P. chlorantha* flower revealed 6280 ovules (Neiland 1994), indicating that average seed production per flower is variable and that output per plant may be higher than expected by Salisbury. Spread of the species by seed dispersal seems to be particularly effective in *Platanthera*. In the United States *Platanthera* species are opportunistic colonizers of roadside verges and excavations (Sheviak 1990; A. L. Jesup, cited in IUCN Orchid Specialist Group 1996) and may form large populations in suitable habitats (e.g. >2000 plants in the study by Carroll *et al.* 1984).

Most germination of *Platanthera* seeds in the field probably takes place in the spring after seed dispersal (Rasmussen 1995), but it may extend throughout the year due to seed dormancy mechanisms, with germination being triggered by some environmental signal such as a period of low temperature (Gregg 1990, cited in Rasmussen 1995). Observations made by Fuchs and Ziegenspeck (1927) indicated that the first apical bud is formed from the protocorm in the autumn and that it produces the leafy shoot the following spring. Shoot formation is followed by emergence of a root from the upper part of the mycorrhizome, which then becomes infected with mycorrhiza. The plant initially overwinters as a short rhizome but in later seasons, at least three years after germination, the first tuber is produced. Some mycorrhizal fungi have been isolated from the roots of *Platanthera* species and identified as *Leptodontidium orchidicola* from *P. orbiculata* and *P. hyperborea* (Currah *et al.* 1987, 1990), *Rhizoctonia anaticula* and *Sistrtrema* species from *P. obtusata* (Banks & Pursh) Lindl. (Smreciu and Currah 1989), *Sebacina vermifera* from *P. orbiculata* (Currah *et al.* 1990), *Rhizoctonia* species from *P. integrilabia* (Correll) Luer (Zettler and Fairey 1990), *Tulasnella calospora* from *P. bifolia* (Allan *et al.* 1993), *Ceratorhiza pernacatena* from *P. praeclara* C.J.Sheviak & M.L.Bowles (Zelmer and Currah 1995), and *Epulorhiza inquilina* from *P. clavellata* (Michx.) Luer, *P. cristata* Lindl., and *P. integrilabia* (Zettler and Hofer 1998). Some of these fungal symbionts have successfully promoted seed germination and protocorm development of *Platanthera* species in experimental trials. It has been suggested that *in vitro* symbiotic seed germination techniques could be applied to the conservation of rare *Platanthera* orchids by producing seedlings, which could be transplanted to field locations (Zettler and McInnis 1992), especially because germination of *Platanthera* seeds through asymbiotic methods can be slow (Rasmussen 1995).

Several members of the genus are rare orchids, and some are protected by national laws, e.g. *P. integrilabia* in the United States (Zettler *et al.* 1996) and *P. obtusata* ssp. *oligantha* (= *P. oligantha* Turcz.) in Norway and Sweden (Hoiland 1990), and may be the focus of active conservation measures. Other more common and widespread *Platanthera* species may be threatened locally by collecting (*P. chlorantha* is collected for use in herbal medicine in China; Chen and Tang 1982), by habitat change including that due to ecological succession, or by different management regimes such as cessation of coppicing or replanting of woodlands, which can detrimentally alter the vegetation composition and light levels of *Platanthera* habitats (IUCN Orchid Specialist Group 1996). **(RN)**

Pollination

As for *Orchis*, spur length is also important in the pollination biology of *Platanthera*. The genus is mainly Lepidoptera-pollinated. European and most North American species have whitish or greenish flowers and are pollinated by hawk-moths or crepuscular moths, but some North American species have purple or yellow-orange flowers and are pollinated by butterflies. A phylogenetic analysis of plant–pollinator interactions in *Platanthera* revealed that pollination by nocturnal settling moths is ancestral and that pollination by hawk-moths, butterflies, bees, or Diptera is derived (Hapeman and Inoue 1997). Detailed studies by Nilsson (1978, 1983*b*) on the European *P. chlorantha* and *P. bifolia* revealed that species boundaries are maintained by placement of pollinaria on different parts of the pollinator's body and differences in pollinator communities. A critical factor for pollination is spur length. If spurs are too short, long-tongued pollinators will not remove pollinaria while visiting flowers. For successful pollination to occur it is therefore necessary that spurs are as long or slightly longer than the pollinators' tongues (Nilsson 1988, 1992, 1998). **(AW, SC, AD)**

Uses

None recorded. **(JW)**

Cultivation

Platanthera is widespread throughout the Northern Hemisphere, often in bogs, woods, and moist areas. North American species may be showy (e.g. *P. ciliaris*) and can grow well in gardens. Many species should thrive in woodland (e.g. *P. dilatata*), shade beds and containers in compost C and D, depending on habitat. Others may be grown in bog and marginal gardens or artificial bogs. **(CB)**

Taxonomic literature

Luer, C. A. (1975). *The native orchids of the United States and Canada excluding Florida*. New York Botanical Garden.

94. PLATYCORYNE

Platycoryne Rchb.f., *Bonplandia*, **3**, 212 (1855); Summerh. in *Kew Bulletin*, **13**, 58–73 (1958). Type species: *P. pervillei* Rchb.f.

Habenaria sect. *Platycoryne* (Rchb.f.) Kränzl., *Bot. Jahrb. Syst.*, **16**, 56, 206 (1893) & *Orch. Gen. Sp.*, **1**, 447–53 (1897).

Derivation of name

From the Greek *platys*, broad, and *koryne*, a club, referring to the broad, thickened rostellum. **(PC)**

Description (Plate 113; Fig. 94.1)

Terrestrial *herbs* with fleshy tubers and leafy, unbranched stems. *Leaves* cauline, lowermost often clustered, those above smaller and grading into the bracts. *Inflorescence* one- to densely flowered, often in short, dense heads; bracts lanceolate, shorter than to as long as the flowers. *Flowers* resupinate, usually yellow or orange, rarely greenish or white. *Sepals* free, the dorsal sepal forming a hood with the petals. *Petals* entire, smaller than the sepals. *Labellum* pendent, entire or three-lobed, spurred; side lobes, if present, usually much shorter than the mid-lobe. *Column* erect, anther erect with parallel loculi, canals adnate to side lobes of rostellum; rostellum large, usually placed in front of anther, which is often overtopped by the mid-lobe; lateral lobes porrect, usually projecting beyond the hood but sometimes short and shoulder-like; stigmatic processes short, thickened with rounded ends. **(PC)**

Distribution (Fig. 94.2)

A genus of 20–25 species in tropical Africa and Madagascar. Most species form colonies in seasonally wet grassland and marshes. **(PC)**

Ecology

Platycoryne species are terrestrial herbs with fleshy or tuberous roots. They usually grow in wet areas such as wet grassland, marshes, seepage zones among rocks, permanently wet dambo, wet vlei, swamps, and land adjacent to streams. *Platycoryne macroceras* Summerh. and *P. isoetifolia* P. J. Cribb are therefore unusual as they grow in drier conditions, in dry grassland or dambo. Some *Platycoryne* species occur in woodland, including *Brachystegia* woodland (e.g. *P. crocea* Rolfe). Substrates in which members of the genus have been recorded to grow include sandy, peaty, and stoney soils, shallow soils overlying laterite or rock, and granite outcrops. Most *Platycorne* species grow at relatively high elevations, ranging from 700–2200 m (la Croix and Cribb 1995), although a few may be found at lower elevations according to Summerhayes (1968). The elevational range of *P. buchananiana* is cited as 550–1850 m and that of *P. mediocris* as 200–1600 m.

Platycorne plants perennate by means of tubers and often form colonies in favourable habitats (la Croix and Cribb 1995). Colonies of the widespread species *P. buchananiana* Rolfe are distinctive in having two colour forms, either orange or yellow. Flowering occurs

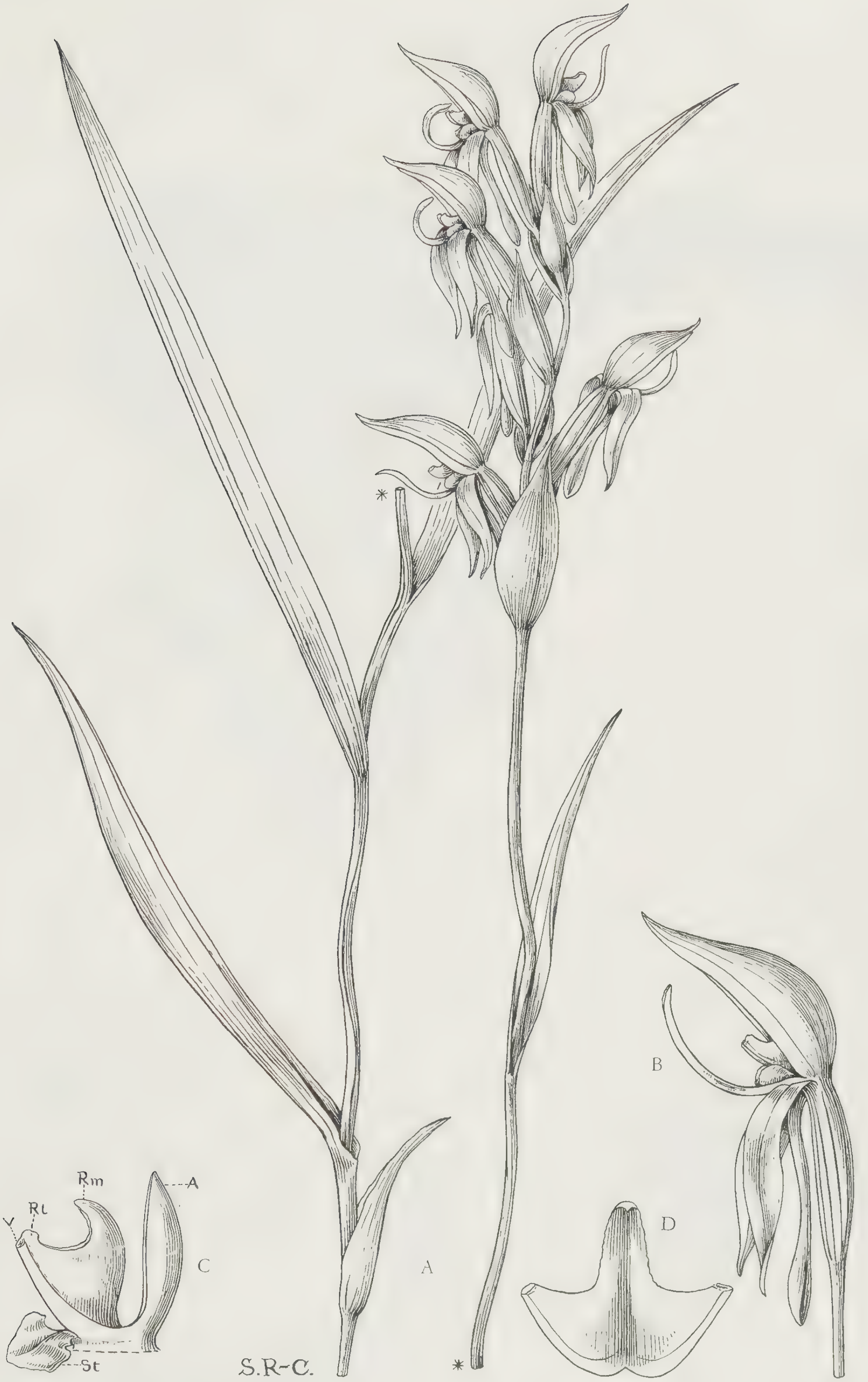

Fig. 94.1. *Platycoryne ambigua* (Kränzl.) Summerh. A. Habit, ×1; B. Flower, side view, ×2; C. Column, side view, ×4; a = anther, rm = rostellum, rl = rostellar lobe, st = stigma, v = viscidium; D. Rostellum, spread, ×4. Drawn by S. Ross-Craig from *Burtt 4261*.

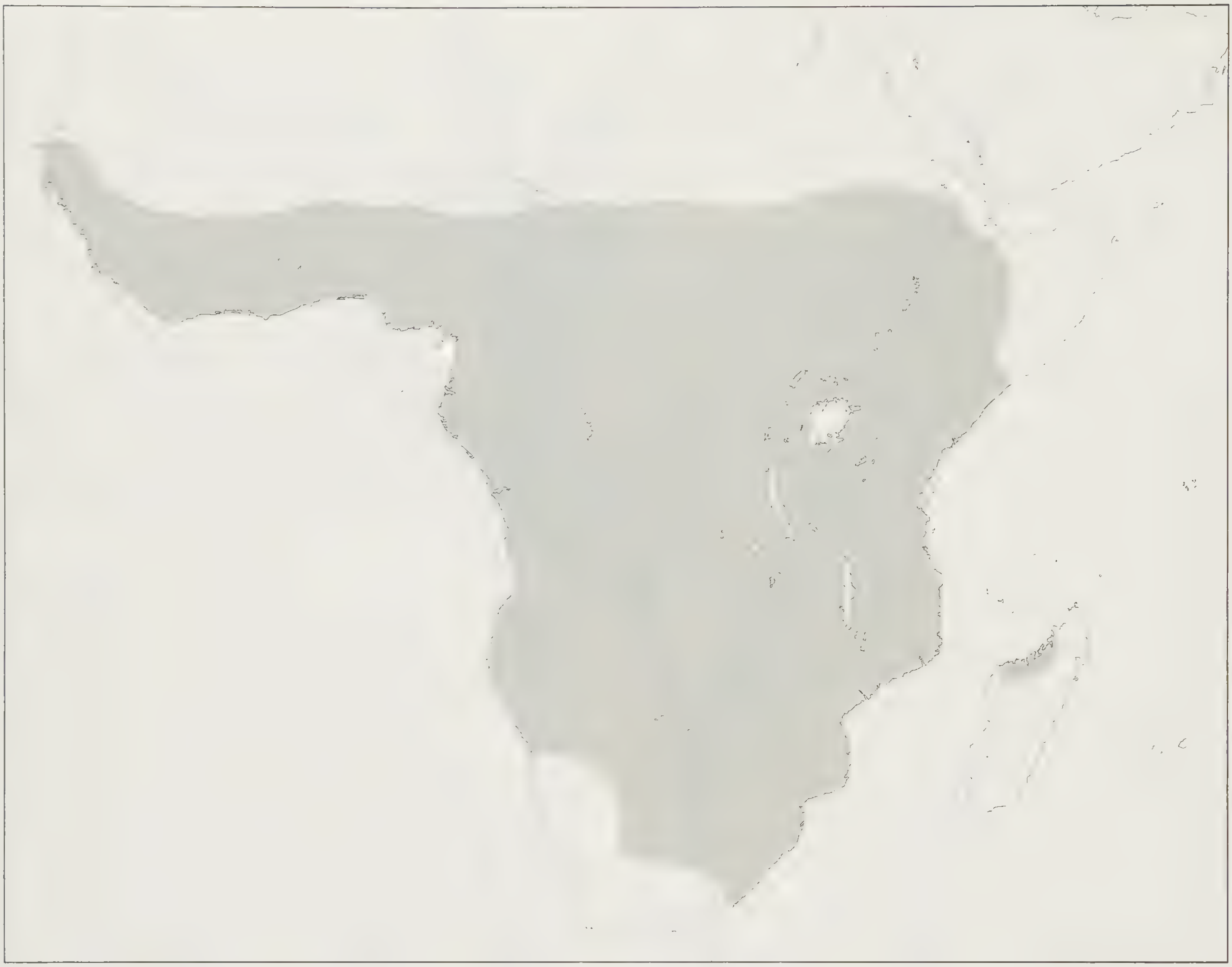

Fig. 94.2. Distribution map of *Platycoryne*.

between October and March, and some fruiting *Platycorne* specimens have been collected from this period as well, such as *P. protearum* Rolfe (la Croix and Cribb 1995). Some members of the genus are narrow endemics such as *P. affinis* Summerh. endemic to Zimbabwe and *P. isoetifolia* endemic to Zambia, whereas others are more widespread, especially *P. crocea* Rolfe, which grows throughout the tropical African range of the genus (Summerhayes 1968; la Croix and Cribb 1995). **(RN)**

Uses

None recorded. **(PC)**

Cultivation

Compost B and D. **(CB)**

Taxonomic notes

Summerhayes (1958) revised the genus recognizing 21 species from Africa and Madagascar. He recognized no infrageneric groupings. Previously, most authors had followed Kränzlin (1893, 1897) in treating *Platycoryne* as a section of *Habenaria*, but Summerhayes disputed this because of: 1) the distinctive habit; 2) the short dense heads of flowers, 3) the mid-lobe of the rostellum which overtops the anther and is usually placed well in front of it; and 4) the rather short, thickened stigmatic lobes. The relationship of *Platycoryne* to *Habenaria sens. lat.* needs further investigation. **(PC)**

Taxonomic literature

Kränzlin, F. (1893). Beiträge zu einer Monographie der Gattung Habenaria Willd. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*, **16**, 52–223.

Kränzlin, F. (1897–1904). *Orchidacearum genera et species.* Mayer & Müller, Berlin.

Summerhayes, V. S. (1958). African orchids, XXV. *Kew Bulletin*, **13**, 57–87.

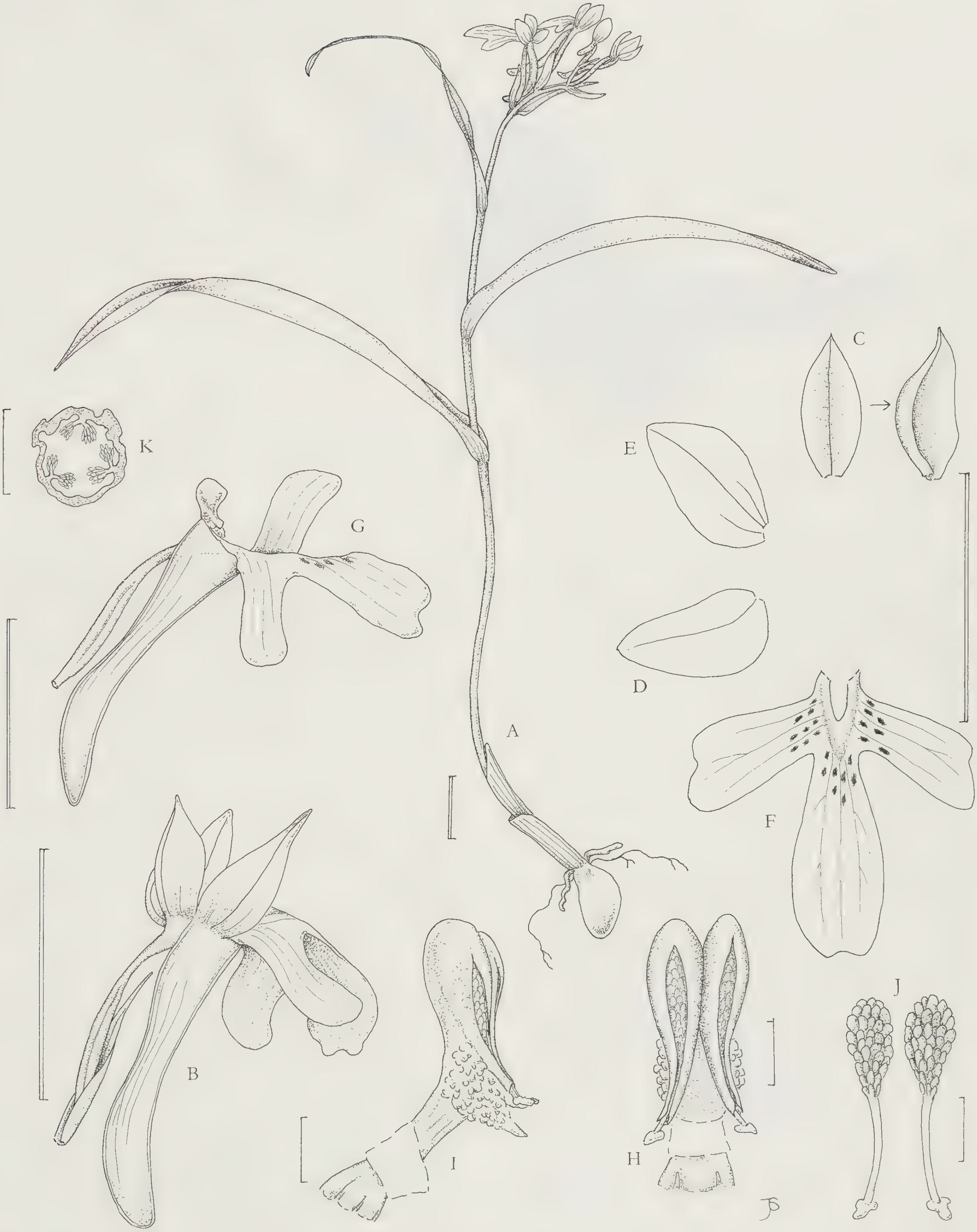

Fig. 95.1. *Ponerorchis graminifolia* Rchb.f. A. Habit; B. Flower; C. Dorsal sepal, front and side views; D. Lateral sepal; E. Petal; F. Labellum; G. Labellum and column; H. Column, front view; I. Column, side view; J. Pollinaria; K. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Furuse 20737.*

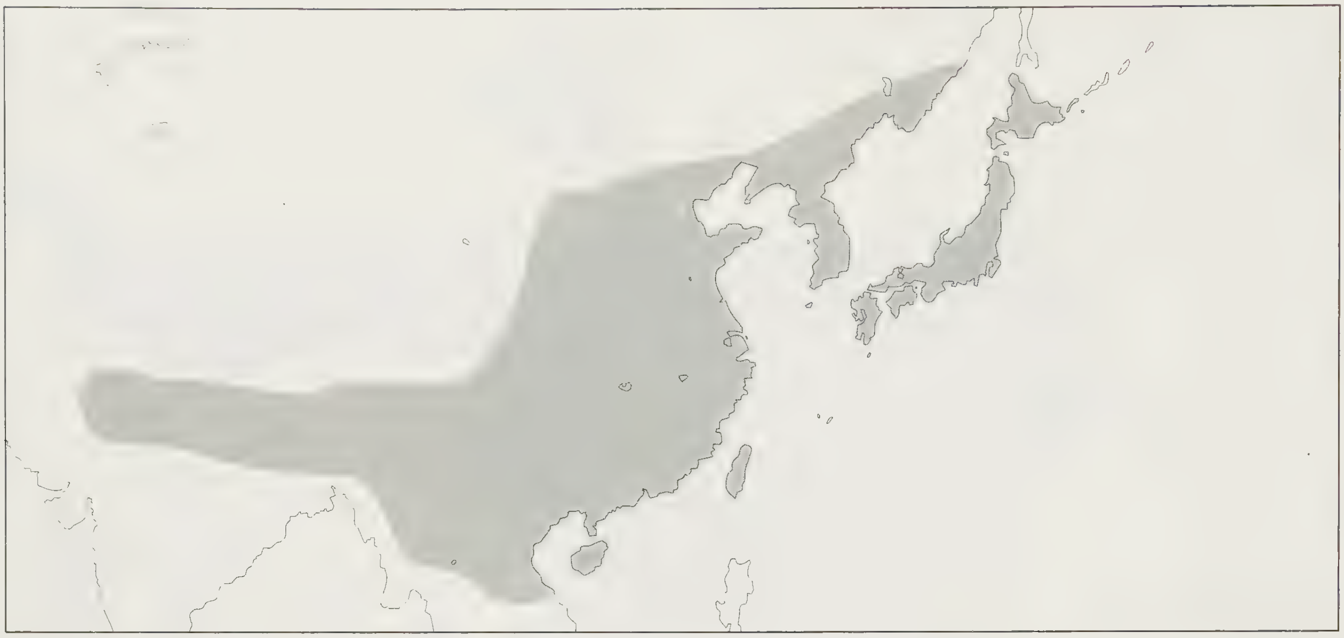

Fig. 95.2. Distribution map of *Ponerorchis*.

95. PONERORCHIS

Ponerorchis Rchb.f., *Linnaea*, **25**, 227 (1852). Type species: *Ponerorchis graminifolia* Rchb.f.

Chusua Nevski in Komarov, *Fl. USSR*, **4**, 670, 753 (1935). Type species: *Chusua donii* Nevski.

Derivation of name

From the Greek *poneros*, worthless, and *orchis*, orchid, an unfortunate label. **(AP)**

Description (Plate 114; Fig. 95.1)

Small to medium-sized, glabrous, terrestrial *herbs* with spherical or oblong tubers. *Leaves* one or two, usually basal. *Inflorescence* laxly to sub-densely flowered; bracts lanceolate, glabrous. *Flowers* pink or purple, rarely yellow, often spotted with darker purple on the lip. *Dorsal sepal* entire, often adnate to the petals forming a hood over the column. *Lateral sepals* similar but spreading. *Petals* entire, smaller than the dorsal sepal. *Labellum* three-lobed, ecallose, spurred at the base; spur more or less as long as the ovary. *Column* short, erect; anther with two more or less parallel loculi; pollinia sectile, clavate; viscidia two, borne in two delicate bursicles; rostellum triangular; stigma concave. *Ovary* subsessile, glabrous. **(PC)**

Distribution (Fig. 95.2)

A genus of about 20 species in the Himalayas, China, and Japan. **(PC)**

Ecology

Members of the genus *Ponerorchis* are inhabitants of grasslands and open shrubland. Cribb (1994) for example, observed *Ponerorchis chusua* (D. Don) Soó growing in meadows on the eastern slopes of the Jade Dragon Snow Mountain in north-west Yunnan, China. The species was said to occur frequently at this locality and grew with other orchids including *Cypripedium* species, *Habenaria glaucifolia* Bureau & Franch., *Gymnadenia orchidis* Lindl., and *Satyrium nepalense* D. Don. *Ponerorchis* can grow from sea level to between 2400 and 4700 m on mountain slopes and flowers from September to October (Polunin and Stainton 1984, noted for *Ponerorchis chusua*). It perennates by means of tubers. **(RN, PC)**

Uses

Ponerorchis graminifolia, a variable species in its floral morphology and coloration, is widely cultivated, especially in Japan. **(PC)**

Cultivation

Ponerorchis species are cultivated in Japan. Compost C or D is recommended. **(CB)**

Taxonomic notes

Most of the species included in *Ponerorchis* were described in *Orchis*, but they differ in having one or two leaves and the viscidia in two delicate bursicles.

Vermeulen (1972) discussed the delimitation of *Ponerorchis* and included *Chusua* in its synonymy. However, recent molecular evidence (Luo and Pridgeon, unpublished) confirms that *Chusua* is distinctly different from *Ponerorchis*. *Chusua* will be treated in a later volume of *Genera Orchidacearum* **(PC)**

Taxonomic literature

Vermeulen, P. (1972). Übersicht zur Systematik und Taxonomie der Gattung *Orchis* s. str. *Jahresberichte des Naturwissenschaftlichen Vereins in Wuppertal*, **25**, 22–36.

Fig. 96.2. Distribution map of *Porolabium.*

96. POROLABIUM

Porolabium T. Tang & F. T. Wang, *Bull. Fan Mem. Inst. Biol. Peiping, Bot, Ser.* 10, **1**, 36 (1940). Type species: *Porolabium biporosum* (Maxim.) T. Tang & F. T. Wang.

Derivation of name

From the Greek *poros*, pore, and Latin *labium*, lip, in reference to the two pore-like glands near the base of the labellum. **(JW)**

Description (Fig. 96.1)

Perennial sympodial *herbs* up to 10 cm high. *Tubers* small, ellipsoid. *Stem* with 2–3 cataphylls. *Leaves* solitary, oblong, obtuse, unspotted. *Inflorescence* sparsely 6- to 8-flowered, erect, terminal; peduncle naked; rachis short; floral bracts minute, broadly ovate to deltoid, obtuse. *Flowers* resupinate, greenish to yellowish green. *Dorsal sepal* broadly ovate, obtuse, connivent with petals to form a hood. *Lateral sepals* ovate-elliptic to obliquely oblong, subacute, spreading to deflexed. *Petals* obliquely ovate, obtuse, erect. *Labellum* spurred, linguiform, entire, dilated at base, with two pore-like glands situated near the base. *Column* short; stigma solitary, undivided, cushion-like, convex, rising out of the cavity, not adnate to rostellum; rostellum prominent, triangular, lateral lobes spreading; anther large, rather cucullate, with a narrow connective and small loculi; pollinia two, attached via caudicles to two viscidia. *Ovary* sessile, twisted. **(JW)**

Distribution (Fig. 96.2)

A monospecific genus narrowly distributed in the mountains of northern China. **(JW)**

Ecology

The monospecific genus *Porolabium* is endemic to the regions of Qinghai and Shansi in Mongolia, China, where it occurs on montane slopes between 3000–3300 m with other terrestrial orchid genera including *Herminium*, *Neottianthe*, *Gymnadenia*, *Orchis*, and *Platanthera* (Chen and Tang 1982). **(RN, JW)**

Uses

None recorded. **(JW)**

Cultivation

Not known in cultivation, but compost C may be tried. **(CB)**

Taxonomic notes

This Chinese orchid was originally placed in *Herminium* by Maximowicz but has been referred to a distinct monospecific genus by Tang and Wang because of the curious pores described at the base of the labellum. The rostellum structure appears to be identical to *Herminium*, and studies of fresh material are required before its generic status can be clarified. **(JW)**

Taxonomic literature

Brieger, F. G., Maatsch, R., and Senghas, K. (1973). 44. *Porolabium.* In *Rudolf Schlechter: Die Orchideen 3. Völlig neubearbeitete auflage* (ed. F. G. Brieger, R. Maatsch, K. Senghas), **4** (13–16), 246–7.

Maximowicz, C. J. (1887). Diagnoses plantarum novarum asiaticarum—VI. Insunt stirpes quaedam nuper in Japonia detectae. In *Bulletin de l'Académie Impériale des sciences de St. Pétersbourg*, **31**, 106.

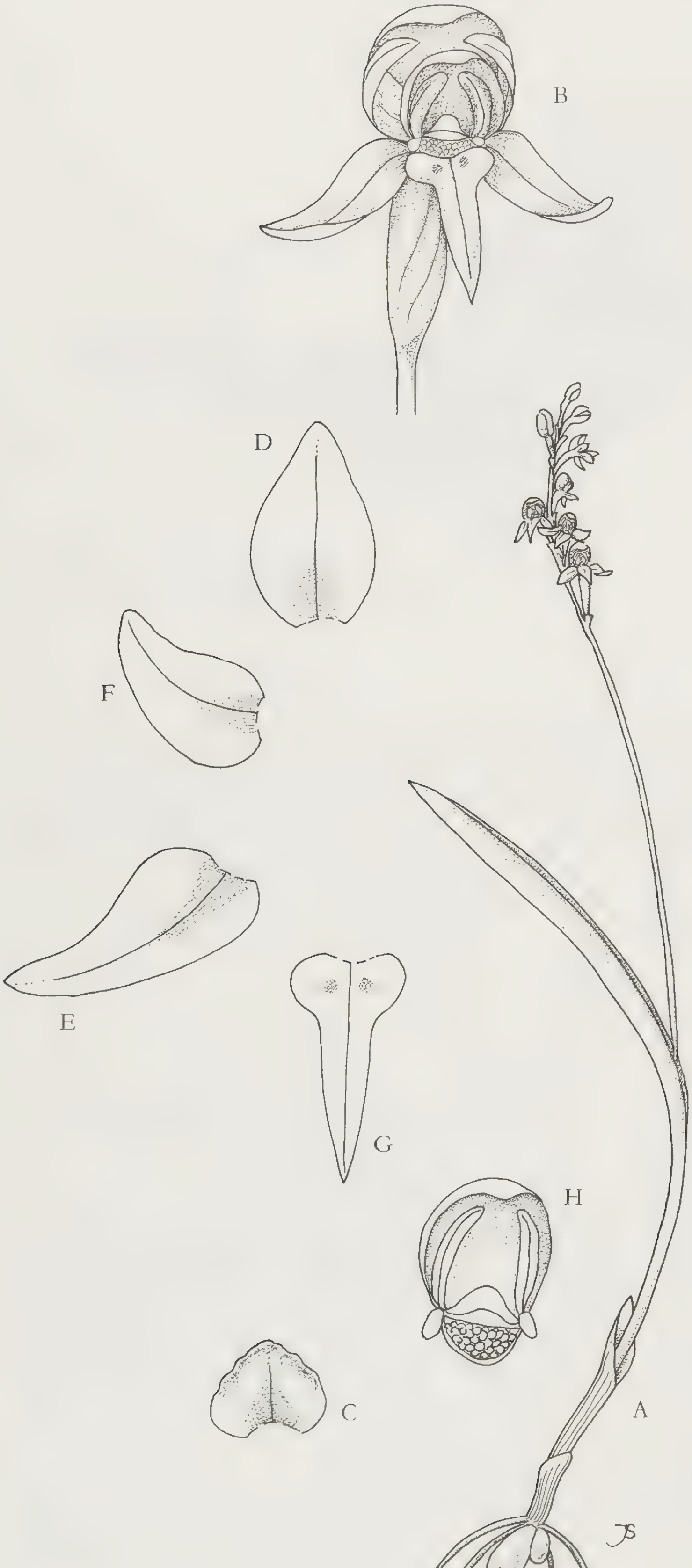

Fig. 96.1. *Porolabium biporosum* (Maxim.) T. Tang & F. T. Wang. A. Habit; B. Flower; C. Bract; D. Dorsal sepal; E. Lateral sepal; F. Petal; G. Labellum; H. Column. Redrawn at ×1.5 by Judi Stone from original drawing by S. Q. Cai.

Tang, T. and Wang, F. T. (1940). Contributions to the knowledge of eastern Asiatic Orchidaceae I. *Bulletin of the Fan Memorial Institute of Biology, Botanical Series*, **10**, 36–8.

97. PSEUDORCHIS

Pseudorchis Ség., *Pl. Veron., Suppl.*, **3**, 254 (1754). Type species: *Pseudorchis albida* (L.) Á. Löve & D. Löve.

Leucorchis E. Mey., *Preuss. Pflanzgatt.*, 50 (1839). Type species: *Leucorchis albida* (L.) E. Mey. (=*Pseudorchis albida* (L.) Á. Löve & D. Löve).

Bicchia Parl., *Flor. Ital.*, **3**, 397 (1858). Type species: *Bicchina albida* (L.) Parl. (=*Pseudorchis albida* (L.) Á. Löve & D. Löve).

Derivation of name

From the Greek *pseudes*, false, and *Orchis*, an orchid genus, alluding to the relationship with *Orchis.* **(JW)**

Description (Plate 115; Fig. 97.1)

Small *herb. Rootstock* tuberous, tubers sessile, bifid to palmate, the slender cylindrical divisions thickened distally. *Stem* erect, leafy. *Leaves* 3–7, oblong-ligulate, obtuse to acute, unspotted. *Inflorescence* cylindrical, densely many-flowered; floral bracts herbaceous, equalling or exceeding ovary. *Flowers* small, resupinate, greenish yellow to whitish. *Sepals* and *petals* connivent, forming a hood. *Labellum* three-lobed, shortly spurred. *Column* suberect; rostellum small, three-lobed; pollinia two, each attached to a small free viscidium. *Ovary* sessile, twisted, glabrous. **(JW)**

Distribution (Fig. 97.2)

A monospecific genus distributed in boreal and temperate Europe and Asia east to Kamtchatka, south to the Pyrenees and Apennines, extending via Iceland and Greenland to Newfoundland. **(JW)**

Palynology

Pollen sculpturing varies in *Pseudorchis albida*, either distinctly hamulate or ornate (Schill and Pfeiffer 1977).. **(AP)**

Phytochemistry

Infection of the tubers of *P. albida* (cited as *Gymnadenia albida* (L.) Rich.) with a strain of *Rhizoctonia repens* from *Orchis militaris* results in the synthesis of the phytoalexin orchinol (2,4-dimethoxy-7-hydroxy-9,10-dihydrophenanthrene) and *p*-hydroxybenzylalcohol (Nüesch 1963; Gaumann *et al.* 1960).

Investigation of the flavonoid content of the leaves of *P. albida* revealed the presence of quercetin and kaempferol. These flavonol aglycones were detected in acid-hydrolysed extracts of leaf tissue, indicating that they originate from flavonol *O*-glycosides (C. A. Williams 1979). **(NV, RG)**

Ecology

Pseudorchis usually grows in full sunlight in rough meadows, pastures, and other impoverished grasslands but can also be found in heathland and open coniferous woods. Although it normally grows in mountain areas at elevations up to 2700 m, it does occur at much lower elevations, such as at sea level on the west coast of Scotland (Allan *et al.* 1993). In Scandinavia two distinct morphological types of *P. albida* have been recognized that show different habitat preferences; they probably immigrated separately into Fennoscandia after the last glaciation. One type grows in open woodlands and hay-meadows in the lowlands and subalpine zone, whereas the other is associated with open mountain habitats in the alpine area (Reinhammar 1995, 1998).

Throughout its distribution, *Pseudorchis* grows on both acidic and calcareous soils, which are usually dry and, if they are damp, are well drained (Summerhayes 1951). *Pseudorchis* plants have a relatively short flowering period, normally from mid-June to mid-July, although this varies according to elevation. High fruit-set, over 90%, has been reported for this nectariferous orchid (Neiland and Wilcock 1998), aided by facultative autogamy at the end of the flowering period (Summerhayes 1951).

Seed germination in the field is said to be high because large populations can sometimes be formed, whereas vegetative propagation of the tubers is thought to make an insignificant contribution to population growth (Summerhayes 1985). The ends of the tubers of *Pseudorchis* are narrow and heavily infected with mycorrhizal fungi, as are its narrow, horizontal roots (Summerhayes 1985). Downie (1959) isolated a fungus from adult plants but was unable to germinate any seeds of *Pseudorchis* with it or any of her test strains of *Rhizoctonia solani* (Rasmussen 1995), although other workers have successfully germinated the seeds asymbiotically using different media (Hadley 1982; Veyret 1969). Following seed germination under natural conditions, an aerial stem does not appear above ground for at least four years (Fuchs and Ziegenspeck 1927, cited in Rasmussen 1995). The foliage leaves remain green throughout the summer and senesce in October (Möller 1987, cited in Rasmussen 1995), but even when in flower it remains a small and inconspicuous orchid.

Pseudorchis is locally common in some areas such as Scandinavia, but especially in the southern parts of its range it is much less frequent and only appears singly or in small populations. *Pseudorchis* can tolerate low levels of shade. In Scotland *P. albida* has been found growing on recently burned grouse moorland among heather (*Calluna vulgaris*), but as the heather grows it becomes less vigorous and eventually disappears (Allan *et al.* 1993). **(RN)**

Pollination

The small flowers of *P. albida* are sweet-scented and offer nectar in a spur (van der Pijl and Dodson 1966). Pollinators have rarely been observed but presumably are moths (van der Pijl and Dodson 1966) or butterflies (Reinhard *et al.* 1991). The possibility that *P. albida* may be autogamous has been raised repeatedly (van der Cingel 1995). **(AW, SC, AD)**

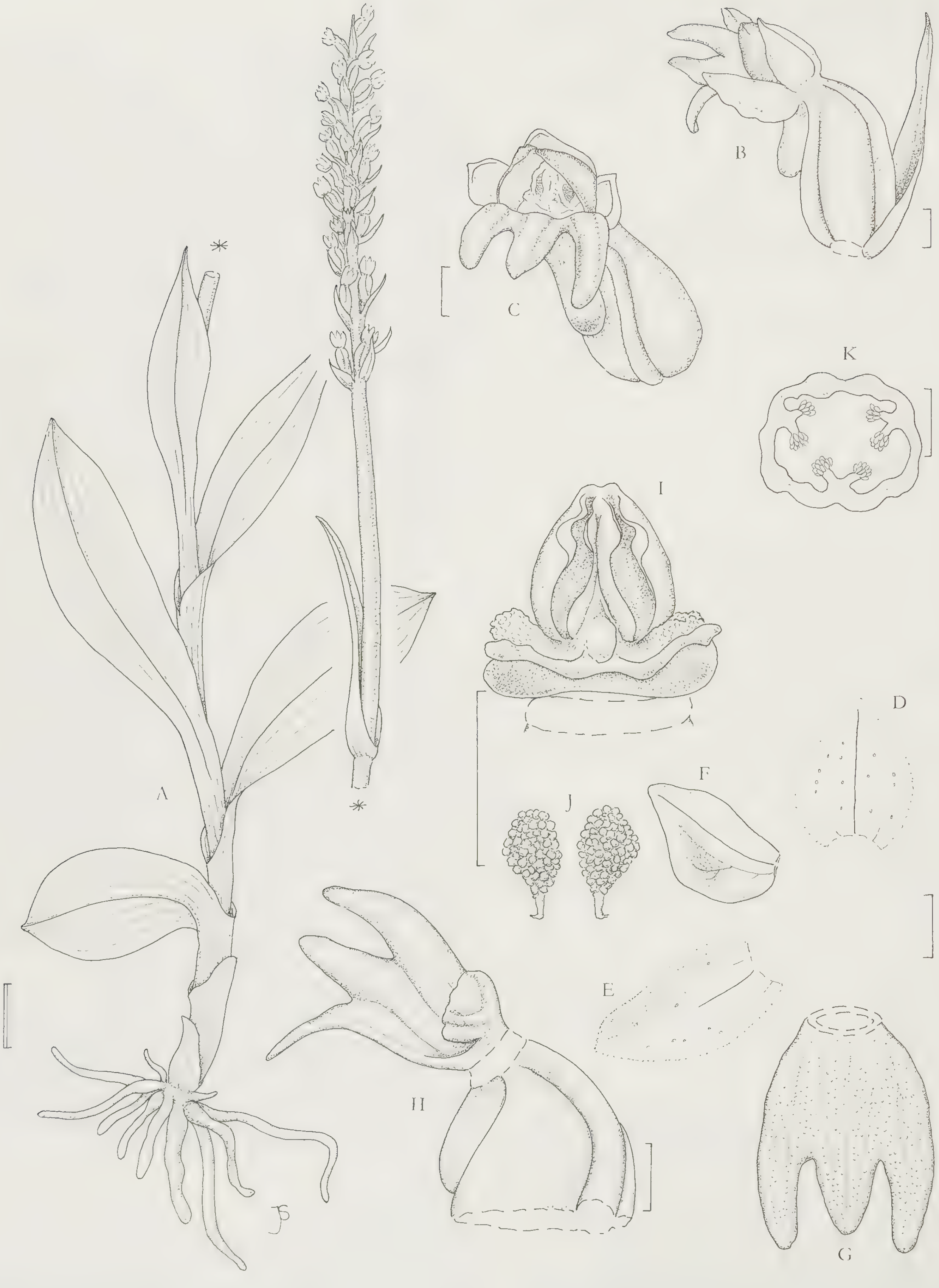

Fig. 97.1. *Pseudorchis albida* (L.) Á. Löve & D. Löve. A. Habit; B. Flower and bract, side view; C. Flower, front view; D. Dorsal sepal; E. Lateral sepal; F. Petal; G. Labellum; H. Labellum and column, side view; I. Column, front view; J. Pollinaria; K. Ovary, transverse section. Single bar = 1 mm; double bar = 1 cm. Drawn by Judi Stone from *Luglio 17* (K) and Kew Spirit Collection no. 40968.

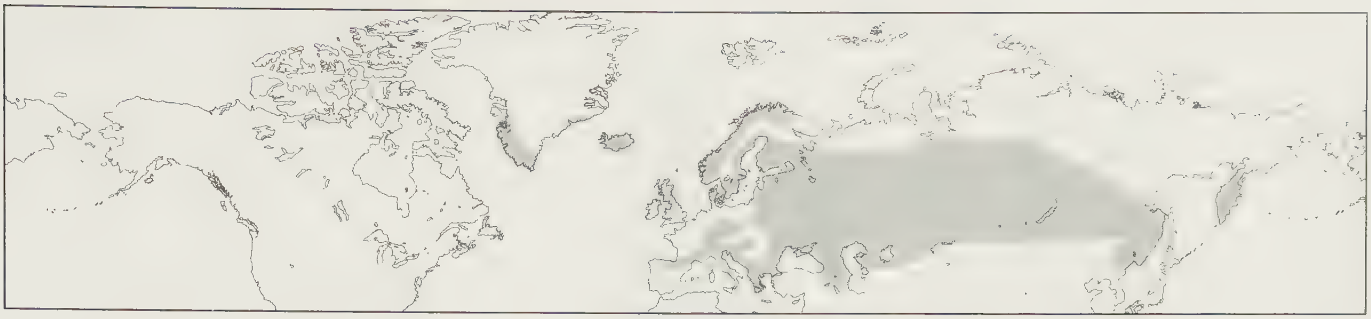

Fig. 97.2. Distribution map of *Pseudorchis*.

Uses

None recorded. **(JW)**

Cultivation

Pseudorchis occurs chiefly in alpine pastures and heathland and also in seepages. Pot in compost C or D depending on habitat. **(CB)**

Taxonomic literature

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98. ROEPEROCHARIS

Roeperocharis Rchb.f., *Otia Bot. Hamburg.*, 104 (1881). Type species: *Roeperocharis bennettiana* Rchb.f. (lectotype selected here)

Derivation of name

Named after Herr Roeper and from the Greek *charis*, grace. Reichenbach described him as a man of 'great merit and pious spirit'. **(PC)**

Description (Plate 116; Fig. 98.1)

Terrestrial *herbs* with tuberous roots. *Stem* leafy, elongate. *Leaves* usually narrow, lanceolate, acute, scattered along the stem, not clustered. *Inflorescence* terminal, sparsely to densely many-flowered. *Flowers* resupinate, green; sepals and petals free. *Sepals* entire, the laterals spreading. *Petals* simple but often toothed or irregular. *Labellum* free, often auriculate at base, three-lobed (rarely entire), with cylindrical spur. *Column* erect, the anther loculi divergent, separated by a broad connective; canals hardly developed; pollinaria two, each with a sectile pollinium, long caudicle and small viscidium; stigmatic processes each two-lobed with one lobe projecting down in front of the labellum base, the other lobe upright in front of the anther connective; rostellum three-lobed, mid-lobe low, rounded or emarginate, adnate to the connective; side lobes spreading, narrowed toward apex. **(PC)**

Distribution (Fig. 98.2)

A genus of five species in eastern Africa, from Ethiopia to Malawi and also in Cameroon. **(PC)**

Ecology

Species of *Roeperocharis* are inhabitants of montane grassland at elevations up to 2440 m. *Roeperocharis bennettiana* Rchb.f. is a robust member of the genus growing up to 100 cm tall, specimens of which have been collected from Nyika National Park in Zambia and Malawi at 2200 m. It tends to grow in drier areas, but other congeneric orchids are usually found in bogs and other wet areas (e.g. *R. wentzeliana* Kränzl.). *Roeperocharis* flower in March and April in south-central Africa (la Croix and Cribb, 1995). **(RN)**

Uses

None recorded. **(PC)**

Cultivation

Cultivation as for tropical *Habenaria*, compost A, B, and D. **(CB)**

Taxonomic notes

Roeperocharis is closely allied to *Habenaria*, distinguished by its column arms with the lobes projecting up and down. However, some *Habenaria* species, such as *H. nigrescens* Summerh. and *H. peristyloides* A. Rich., closely approach *Roeperocharis* in floral morphology yet lack the column arms. Their relationship needs further investigation. **(PC)**

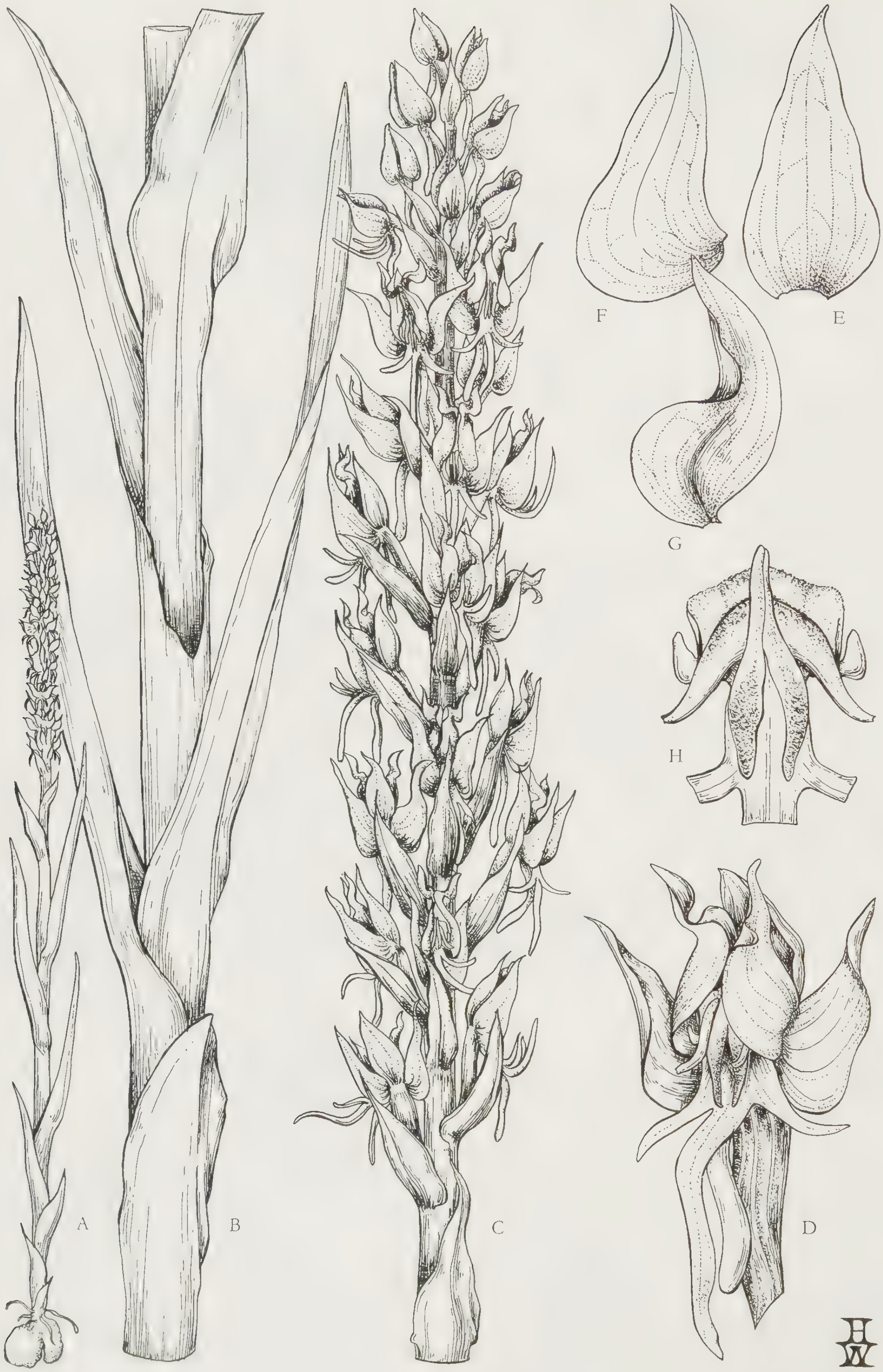

Fig. 98.1. *Roeperocharis bennettiana* Rchb.f. A. Habit, ×0.5; B. Stem, lower portion, ×1; Inflorescence, ×1; C. D. Flower, oblique view, ×2; E. Dorsal sepal, ×3; F. Lateral sepal, ×3; G. Petal, ×3; H. Column, front view, sepals and petals removed, ×3. Drawn by Heather Wood from *Stolz 2492* and *Holmes 227*.

Fig. 98.2. Distribution map of *Roeperocharis*.

99. SCHIZOCHILUS

Schizochilus Sond., *Linnaea*, **19**, 78 (1847). Type species: *S. zeyheri* Sond.

Derivation of name

From the Greek *schizein*, split, and *cheilos*, lip, probably referring to the three-lobed lip. **(PL, HK)**

Description (Plate 117; Fig. 99.1)

Slender terrestrial *herbs* with testicular tubers and a few unbranched roots. *Stem* to 80 cm tall, glabrous, green, erect. *Leaves* basal and/or cauline, linear to rarely elliptic, narrowly oblanceolate or ovate, acute, glabrous; lower leaves 5–30, usually semi-erect with a prominent midrib; cauline leaves smaller, above grading into the floral bracts. *Inflorescence* terminal, sparse to dense, usually nodding; bracts green, acuminate, ovate to narrowly lanceolate, generally as long as the ovaries. *Flowers* non-resupinate, 1.5–10 mm in diameter, white, white and yellow, yellow, or white with a mauve or pink tint. *Dorsal sepal* narrowly to broadly elliptic or elliptic-oblong to rotund, often apiculate, shallowly galeate. *Lateral sepals* suboblique, lanceolate to ovate, more or less acute, slightly larger than the dorsal sepal. *Petals* 1/3–2/3 as long as the sepals, single-veined, oblique, usually more or less rhomboid and acute, free from the lip and column. *Labellum* as long as the sepals, the epichile more or less three-lobed with the central lobe longer than the lateral lobes; hypochile concave, leading into the spur, frequently with calli between the hypochile and epichile; spur cylindrical to bifid, slender to clavate, always shorter than the lip, generally straight. *Column* erect, slender; anther thecae erect or angled to 45°, parallel and adjacent; lateral appendages small; pollinia sectile, with short caudicles and two small naked viscidia; stigma flat, above the entrance to the spur; rostellum three-lobed with small central lobe, lateral lobes square, carrying the viscidia. **(PL, HK)**

Distribution (Fig. 99.2)

Schizochilus comprises 11 species in the summer-rainfall region in southern and south-central Africa as far north as southern Tanzania. **(PL, HK)**

Phylogenetics

Schlechter (1895) allied *Schizochilus* with the *Gymnadenia–Platanthera* group on the basis of lip structure, general tepal orientation, and rostellum structure. This system was followed for the next 100 years

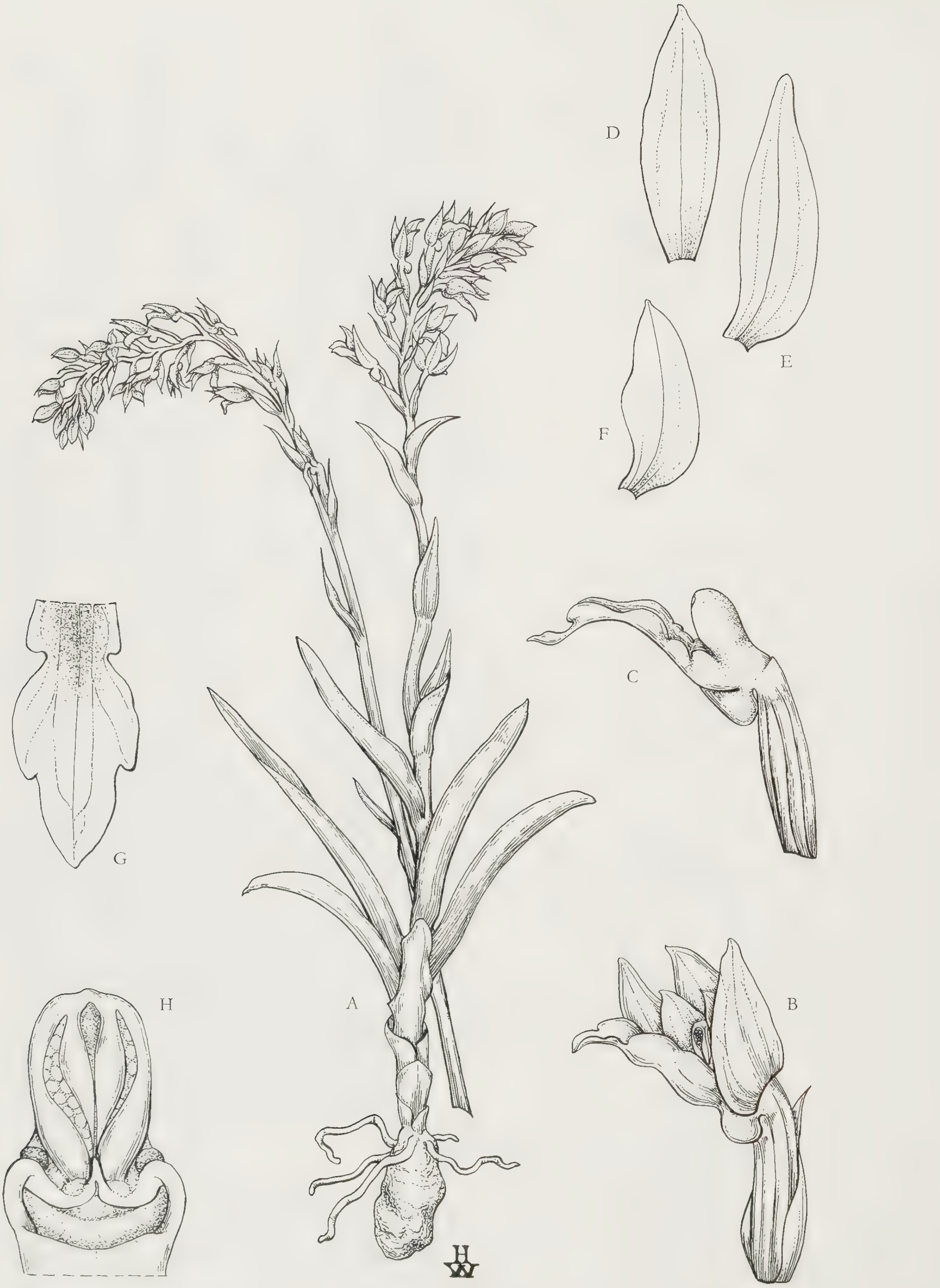

Fig. 99.1. *Schizochilus sulphureus* Schltr. A. Habit, ×1; B. Flower, ×4; C. Labellum, column, and ovary (sepals and petals removed), side view, ×4; D. Dorsal sepal, ×5; E. Lateral sepal, ×5; F. Petal, ×5; G. Labellum, ×5; H. Column, front view (labellum removed), ×15. Drawn by Heather Wood from *Stolz 1075* and *Ball 795*.

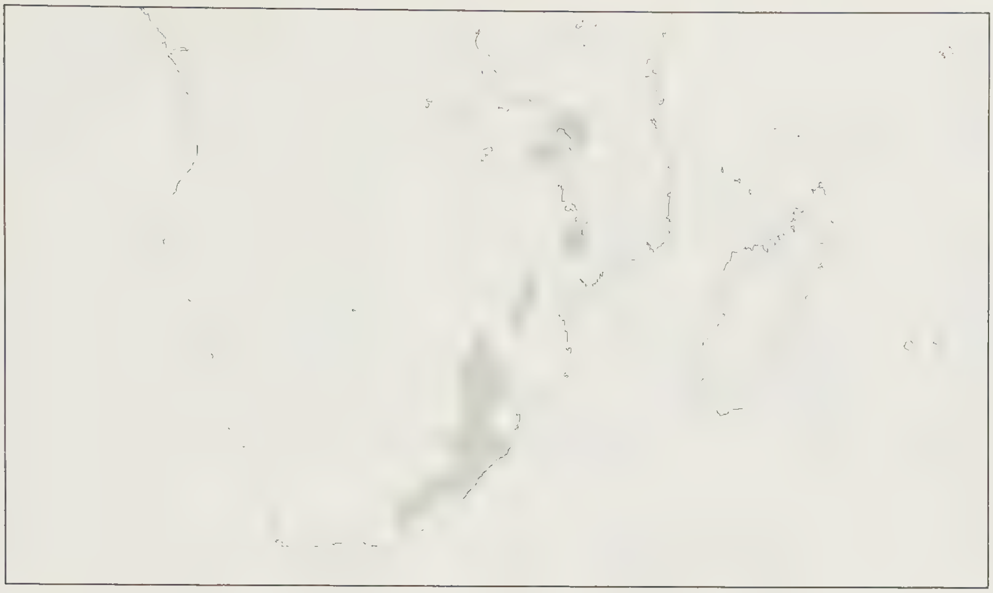

Fig. 99.2. Distribution map of *Schizochilus.*

(Kränzlin 1898; Schlechter 1921, 1927; Summerhayes 1968; la Croix and Cribb 1995). To date, there has been no critical phylogenetic analysis of this group. Within southern Africa the affinities of the genus are clearly with *Brachycorythis*, *Neobolusia*, and *Dracomonticola.*

The differentiation of *Schizochilus* from its allied genera may be difficult, but the genus can usually be distinguished by the nodding inflorescences (a rare feature in this group of genera) and the petals, which are only about half the length of the sepals. Short petals are also found in *Dracomonticola* but not in *Brachycorythis* and *Neobolusia.*

Linder (1980) discussed the evolution within the genus in some detail. The genus is centred along the eastern escarpment mountains of southern Africa, with centres in the KwaZulu-Natal Drakensberg, the mountains of Mpumalanga, the eastern highlands of Zimbabwe, and the mountains around Lake Malawi. He suggested that much of the differentiation in the genus could be related to elevational differentiation, associated with adaptation to different habitats in the montane grasslands. Linder also postulated an evolutionary scenario for the genus, based on *S. zeyheri* as the 'primitive' species, with the remaining species being modifications of the basic floral structure shown by *S. zeyheri*. However, there is as yet no cladistic analysis available for the genus, against which these ideas can be tested. **(PL, HK)**

Ecology

The typical habitat of *Schizochilus* is damp montane grassland where it often grows in shallow soils and in moss seepages over rocks, usually at elevations ranging from 1500 to 3000 m. Localities for the genus include the high-rainfall areas of eastern South Africa, but some species have also been recorded at much lower elevations on the Transkei coast (Schelpe 1966). *Schizochilus* perennates by means of tubers and usually flowers in the spring or summer, often appearing after fire. Populations of the dimorphic species, *S. cecilii* Rolfe, are unusual in that they may include both white and yellow flower colour forms (la Croix and Cribb 1995). In a recent survey for the IUCN (IUCN Orchid Specialist Group 1996) P. Linder cited potential afforestation of montane and mid-elevation grasslands as a principal risk to survival of some *Schizochilus* species such as the endemic *S. gerrardii* (Rchb.f) Bolus, which is, restricted to one area of grassland in northern Natal (Linder 1980).

Within the range of the genus, some taxa have restricted distributions. *Schizochilus cecilii* subsp. *cecilii* is known only from the area of Nyanga in Zimbabwe, and *S. calcaratus* Cribb & la Croix is found only in the Chimanimani Mountains. Other species are more widespread, such as *S. sulphureus*, which occurs in mountains and plateaus in Malawi and Mozambique and the southern highlands of Tanzania (la Croix and Cribb 1995). **(RN)**

Uses

None recorded. **(PC)**

Cultivation

Species of *Schizochilus* grow at high elevations in grassland and damp areas. Compost C or D. **(CB)**

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100. SERAPIAS

Serapias L., *Sp. Plant.*, ed. 1, 949 (1753). Type species: *Serapias lingua* L.

Derivation of name

Dedicated indirectly to the Egyptian god *Serapis* in whose temple pilgrims engaged in licentious living. The name was applied by the Greeks to an orchid, probably *Orchis morio*, which was reputedly an aphrodisiac. **(JW)**

Description (Plate 118; Fig. 100.1)

Rootstock tuberous, tubers 2 or 3(–5), ovoid to globose, entire, sessile or stipitate. *Stem* glabrous. *Leaves* narrowly linear to broadly lanceolate, erect or sometimes folded and curved, cauline, with spotted or unspotted sheathing bases. *Inflorescence* usually elongate, sparse to dense, 2–10(–20)-flowered; floral bracts conspicuous, large, leafy, mostly exceeding flowers, with numerous longitudinal nerves. *Sepals* and *petals* connivent to form an acute to acuminate hood. Sepals narrowly elliptic to ovate-elliptic, free at apex. Petals ovate-elliptic, ovate-subulate, tapering to a long fine point. *Labellum* spurless, three-lobed, usually broader and longer than sepals, divided into a basal hypochile with erect side lobes and bearing two ridge-like calli arising laterally from lower edges of stigmatic cavity, extending on to a hirsute disc, or a single basal callosity (*S. lingua* group), and a distal tongue-like, narrowly elliptic to broadly ovate or cordate, three-nerved, pendent or recurved epichile. *Column* elongate, directed obliquely forward; anther-connective prominent, 7(–10) mm long; stigmatic cavity elongate or circular; rostellum small; pollinia two, each with a caudicle attached to a single viscidium placed in a simple bursicle. Ovary cylindrical to fusiform, sessile, not twisted, glabrous. **(JW)**

Distribution (Fig. 100.2)

An essentially Mediterranean genus of 19 currently recognized species distributed from the Azores and Canary Islands in the west to the Caucasus in the east, south to North Africa and north as far as Brittany in France. *Serapias lingua* was recently recorded from Guernsey in the Channel Islands, and *S. parviflora* has been found in Cornwall, England. **(JW)**

Infrageneric treatment (JW)

Nelson (1968) recognized two sections in the genus as follows:

Serapias section **Bilamellaria** Schltr., *Feddes Repert.*, **19**, 37 (1923). Type species: *S. vomeracea* (Burm.f.) Briq., including all the species with two calli at the base of the lip.

Serapias section **Serapias.** Type species: *S. lingua* L., including those species with a single callus ridge.

Palynology

Pollen sculpturing of *S. lingua*, *S. olbia* Maire & Stephenson, and *S. vomeracea* is consistently hamulate. Free-standing baculae are rare (Schill and Pfeiffer 1977). **(AP)**

Cytogenetics

Chromosome numbers of investigated species are all $2n = 2x = 36$, with the exception of *S. lingua* with $2n = 4x = 72$ (Del Prete 1977, 1978; Mazzola *et al.* 1982; Cauwet-Marc and Balayer 1986; Bianco *et al.* 1987; Bianco *et al.* 1990; D'Emerico *et al.* 1992). All the taxa investigated have frequent secondary constrictions, located on the long arm (Fig. C.2d). The karyotypes are moderately asymmetrical with predominantly submetacentric and subtelocentric chromosomes. A comparison of the complements of *S. vomeracea* and *S. vomeracea* subsp. *laxiflora* showed that their chromosomes are similar. Moreover, the karyotypes of *Serapias parviflora* and *S. politisii* are similar and characterized by low asymmetry indices. *Serapias*

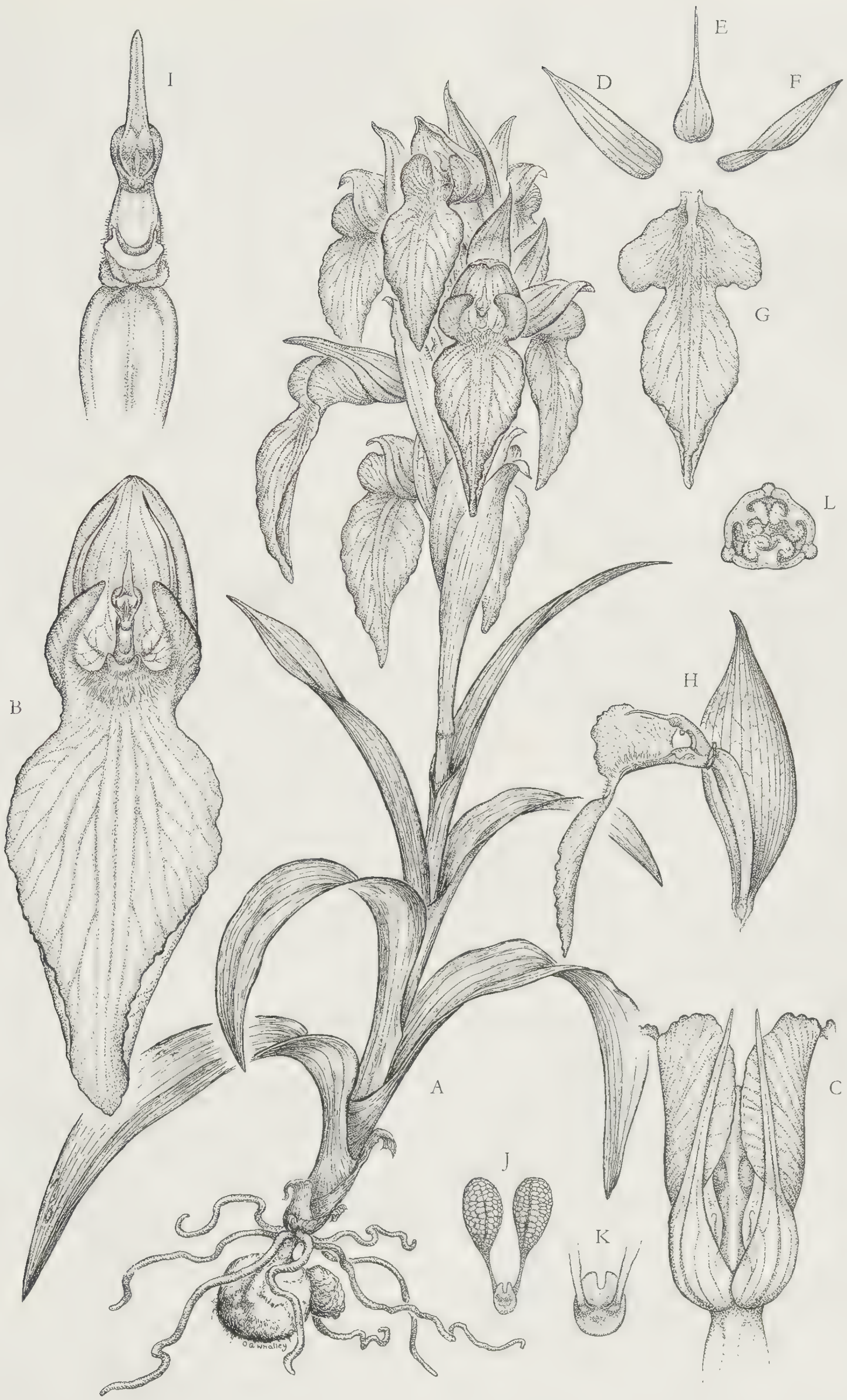

Fig. 100.1. *Serapias neglecta* De Not. A. Habit, ×1; B. Flower from front, ×3; C. Flower from above, ×3; D. Dorsal sepal, ×1; E. Petal, ×1; F. Lateral sepal, ×1; G. Labellum from above, ×1; H. Column and bract from side (one lobe of labellum removed), ×1; I. Column from front, ×6; J. Pollinarium, ×6; K. Viscidium and base of caudicles, ×15; L. Ovary, transverse section, ×4.5. Drawn by Oliver Q. Whalley from Kew Spirit Collection nos. 39558, 46527, and 40610.

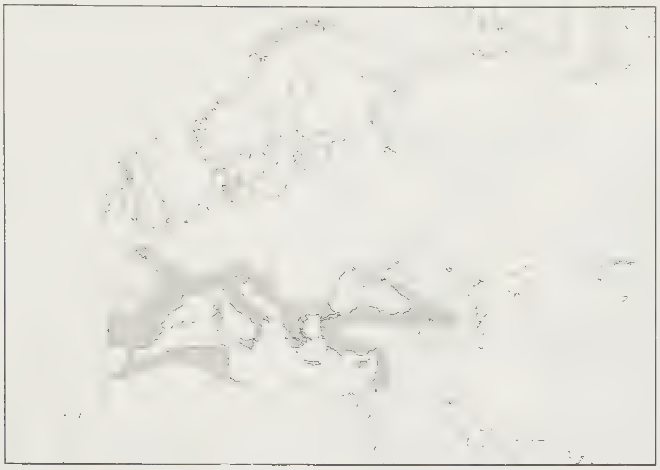

Fig. 100.2. Distribution map of *Serapias.*

apulica has a more asymmetrical karyotype than the other taxa (D'Emerico *et al.* 1990, 1992).

Serapias species have a high number of conspicuous bands located at centromeric positions; in addition some chromosome pairs have C-bands at telomeric position on the short arms (Fig. C.4d). The taxa investigated are characterized by different amounts of heterochromatin (D'Emerico *et al.* 1997). **(SD)**

Phytochemistry

Infection of the tubers of *S. lingua*, *S. neglecta* De Not., and *S. vomeracea* with a strain of *Rhizoctonia repens* from *Orchis militaris* results in the synthesis of the phytoalexin orchinol (2,4-dimethoxy-7-hydroxy-9,10-dihydrophenanthrene) and *p*-hydroxybenzylalcohol. This observation was made as part of a survey of orchinol and *p*-hydroxybenzylalcohol production in a number of species representing genera in subtribe Orchidinae (Nüesch 1963; Gaumann *et al.* 1960).

Investigation of the flavonoid content of leaves of *S. cordigera* L., *S. lingua*, and *S. vomeracea* revealed the presence of the flavonol quercetin. In addition, the leaves of *S. cordigera* and *S. vomeracea* contain the flavonol kaempferol. These flavonol aglycones were detected in acid-hydrolysed extracts of leaf tissue, indicating that they originate from flavonol *O*-glycosides (C. A. Williams 1979). A preliminary examination of the anthocyanin content of *S. lingua* flowers indicated that they contain cyanidin 3-glucoside (chrysanthemin), cyanidin 3-diglucoside (mecocyanin), cyanidin 3, 5-diglucoside (cyanin), and the pigments orchicyanin I and II (Uphoff 1979). Six further species were investigated by Strack *et al.* (1989), who found that the predominant anthocyanins of *Serapias* flowers are cyanidin 3,7-diglucoside (seranin) and cyanidin oxalyl-3,7-diglucoside (serapianin).

Baytop and Sezik (1968) reported on the chemical analysis of tubers of *S. laxiflora* and *S. vomeracea* collected in south-west Anatolia, Turkey. Their results were summarized in a later review by Ernst and Rodriguez (1984). See *Anacamptis.* **(NV, RG)**

Ecology

Members of the Mediterranean genus *Serapias* grow on alkaline to slightly acid soils, normally with a pH of 6.5–8.0 and a low ion content (Vöth 1976, cited in Rasmussen 1995). *Serapias* species grow in both dry and wet soils in a range of habitats including dry grasslands and shrublands, damp pastures and meadows, sand-dune slacks, cultivated terraces, olive groves, and open coniferous woodlands (Delforge 1995; Davies *et al.* 1988). Apart from *S. neglecta*, which is restricted to coastal areas below 600 m, most species of the genus can grow at relatively high elevations of up to 1200 m (Delforge 1995).

Serapias typically flowers from March to May and outside the Mediterranaean may flower even later in June (Delforge 1995). A rosette of winter-green leaves is formed the previous autumn, from which the inflorescence develops in spring with the flowers opening as the spike elongates (Rasmussen 1995). Fruit-sets ranging from 40%–90% have been recorded among *Serapias* populations in southern Portugal (Neiland 1994), which are high given that the genus is nectarless (Neiland and Wilcock 1998).

Following dispersal of seeds plants of *Serapias* senesce completely and survive the dry summer season in the Mediterranean as tubers (Fuchs and Ziegenspeck 1927, cited in Rasmussen 1995). The juvenile stage may be relatively short in *Serapias* because, in culture, 60% of plants have been found to flower three years after sowing under glasshouse conditions (Vöth 1976, cited in Rasmussen 1995). Seedling development in the field is probably assisted by endophytes, and species of *Serapias* have been shown to be compatible at least with *Tulasnella*-like fungi at this stage in their life history (Clements *et al.* 1986). *Serapias* may form large colonies on suitable sites, but some species remain quite rare, such as *S. neglecta* and *S. parviflora* (Davies *et al.* 1988; Delforge 1995). **(RN)**

Pollination

The petals of *Serapias* form a tube that varies in size among species and is used by pollinators, mainly bees, as a shelter (Dafni *et al.* 1981). Beetles have also been found in flowers of *S. olbia* and *S. neglecta* subsp. *neglecta*. Pollination presumably is not specific because tube diameter seems to be the only factor regulating access to the flowers and thus to the pollinaria. The role of scent in pollinator attraction to *Serapias*, however, has not been explored in detail (van der Cingel 1995). **(AW, SC, AD)**

Uses

Tubers of some species are collected in several eastern Mediterranean countries and parts of the Middle East for the production of salep. **(JW)**

Cultivation

Habitats vary from roadsides and meadows to marshes and pine woods. *Serapias* is not hardy in northern Europe but may form sizable colonies in containers or frames. Pot in compost C. **(CB)**

Taxonomic notes

Serapias is an isolated and quite distinct monophyletic genus with closely related species, the delimitation of which varies among authors. It is clear, however, that several taxa exhibit a cline of variation with characters that overlap in areas of their range. The abundance of transitional forms and the tendency for populations to vary in aspect during the same season and from year to year has resulted in much confusion.

Renz and Taubenheim (1984) stated that in Turkey the genus shows a continuous range of variation such that unequivocal distinctions among the taxa are in many cases unsatisfactory. Taxa at each end of the range are indicated by parentheses: (*S. cordigera*)–*S. vomeracea* subsp. *orientalis*–*S. vomeracea* subsp. *laxiflora*–(*S. parviflora*).

Several new taxa have been proposed in recent years, but many of these likely represent only extremes in clines of variation. **(JW)**

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101. SMITHORCHIS

Smithorchis T. Tang & F. T. Wang, *Bull. Fan Mem. Inst. Biol., Bot.*, **7**, 139 (1936). Type species: *S. calceoliformis* (W. W. Sm.) T. Tang & F. T. Wang.

Derivation of name

Named in honour of Professor Sir William Wright Smith (1875–1956), Regius Keeper of the Royal Botanic Garden, Edinburgh, who contributed widely to our knowledge of the flora of China. **(JW)**

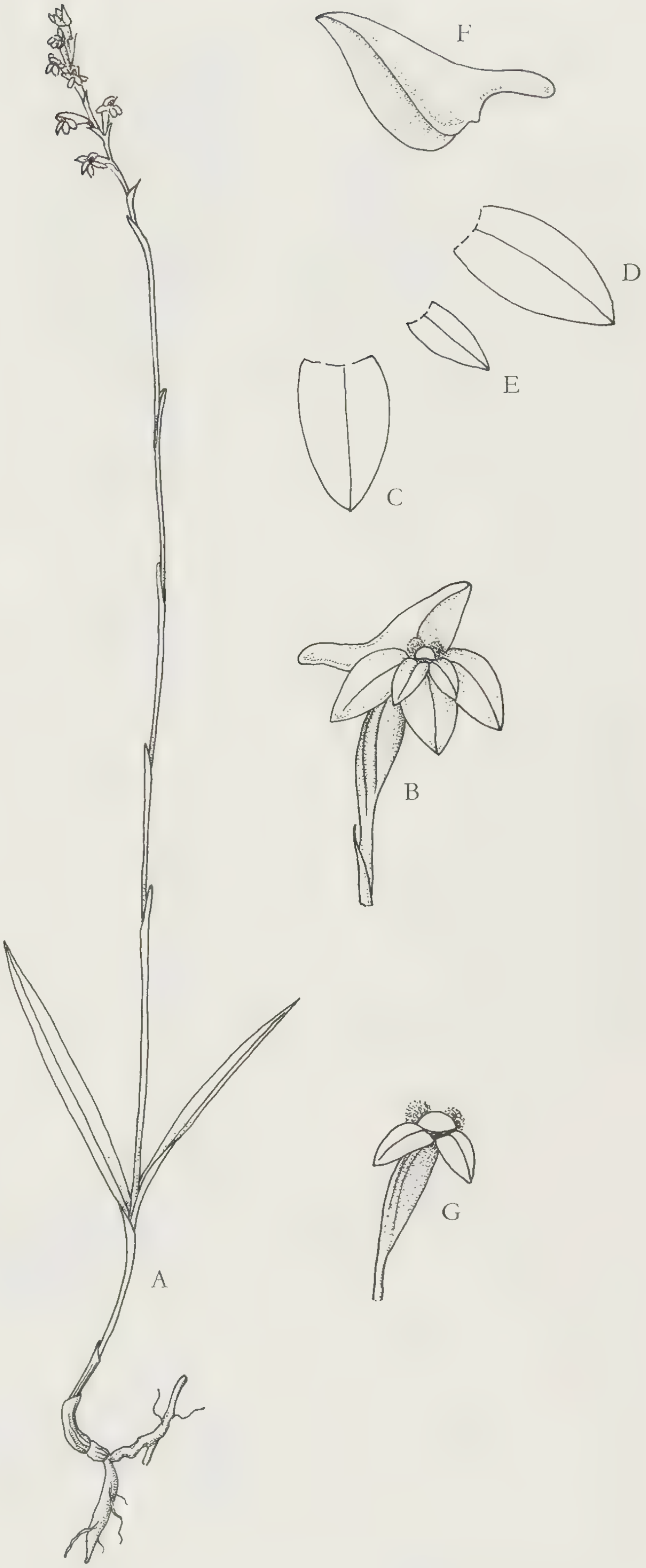

Fig. 101.1. *Smithorchis calceoliformis* (W. W. Sm.) T. Tang & F. T. Wang. A. Habit; B. Flower; C. Dorsal sepal; D. Lateral sepal; E. Petal; F. Labellum; G. Column, petals, and ovary. Redrawn at ×1.5 by Judi Stone from original drawing by S. Q. Cai.

Description (Fig. 101.1)

Terrestrial, erect *herb* 5–10 cm high, with a narrow, creeping rhizome. *Stem* 2–4 leaved. *Leaves* borne toward base of stem, narrowly elliptic, acute, narrowly petiolate, unspotted. *Inflorescence* terminal, racemose, sparsely 6–9-flowered; peduncle with four or five non-floriferous bracts; rachis *c.* 1.5 cm long; floral bracts linear-lanceolate, shorter than flowers. *Flowers* non-resupinate, tipped dull orange, fragrant. *Sepals* free, membranous, similar in size. *Petals* smaller than sepals. *Labellum* superior, concave, slipper-shaped, entire, with a short saccate spur, adnate to column at base. *Column* short; rostellum small, undifferentiated and united with the entire stigma into a uniform suborbicular structure; lateral appendages tiny; anther sessile, cucullate, erect, loculi parallel, canals absent; pollinia granular, caudicles absent (or very short?); viscidia flat, orbicular. **(JW)**

Distribution (Fig. 101.2)

A monospecific genus endemic to the mountains of Yunnan in south-west China. **(JW)**

Ecology

Smithorchis calceoliformis is found in open, stony pastures between 3200–3600 m. **(JW)**

Uses

None recorded. **(JW)**

Cultivation

Not known in cultivation, but compost C or D may be tried. **(CB)**

Taxonomic notes

The sole representative of this genus, *S. calceoliformis*, was originally placed in *Herminium* by W. W. Smith, certain species of which it resembles in habit. Tang and Wang (1936) considered it closest to *Diphylax*, which differs in having a distinct rostellum, larger viscidia, and elongate staminodes. **(JW)**

Taxonomic literature

Brieger, F. G., Maatsch, R., and Senghas, K. (1973). 45. *Smithorchis.* In *Rudolf Schlechter: Die Orchideen 3. Völlig neubearbeitete auflage* (ed. F. G. Brieger, R. Maatsch, K. Senghas), **4**, 247.

Smith, W. W. (1921). New orchids from Yunnan and northern Burma. *Notes from the Royal Botanic Garden, Edinburgh*, **13**, 211–12.

Ying, T., Zhang, Y., and Boufford, D. E. (1993). *The endemic genera of seed plants of China.* Science Press, Beijing.

102. STENOGLOTTIS

Stenoglottis Lindl., *Companion Bot. Mag.*, **2**, 209 (1837). Type species: *S. fimbriata* Lindl.

Derivation of name

From the Greek *stenos*, narrow, and *glotta*, a tongue, in allusion to the narrow and lacerate lip of the type species. **(PC)**

Description (Plate 119; Fig. 102.1)

Terrestrial, lithophytic or epiphytic *herbs* with swollen fleshy roots, lacking tubers. *Leaves* several to many, in a basal rosette. *Inflorescence* erect with a few scattered sheaths, an erect lax or dense raceme;

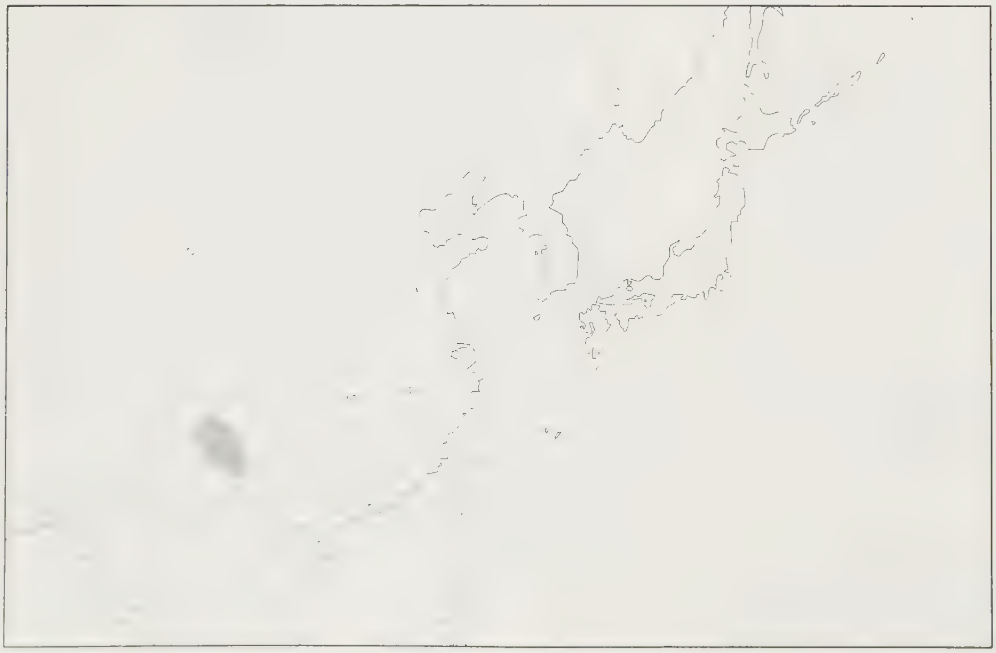

Fig. 101.2. Distribution map of *Smithorchis.*

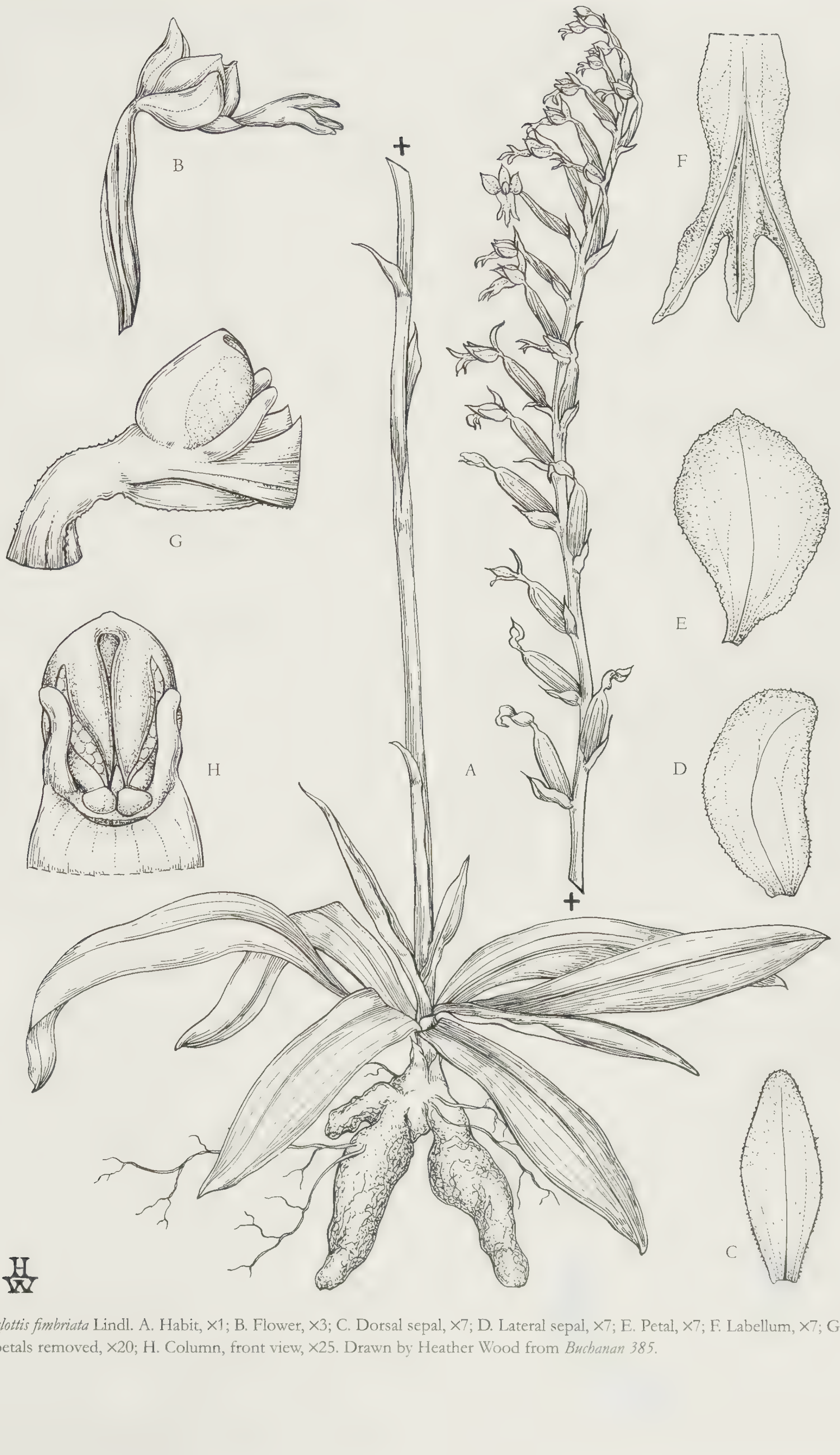

Fig. 102.1. *Stenoglottis fimbriata* Lindl. A. Habit, ×1; B. Flower, ×3; C. Dorsal sepal, ×7; D. Lateral sepal, ×7; E. Petal, ×7; F. Labellum, ×7; G. Column, side view, sepals and petals removed, ×20; H. Column, front view, ×25. Drawn by Heather Wood from *Buchanan 385*.

bracts small, shorter than ovary. *Flowers* numerous, sometimes subsecund, white, pink or lilac, usually with darker spots. *Sepals* briefly united to base of column and labellum, otherwise free, entire. *Petals* erect, entire, oblique. *Labellum* spurred or unspurred, longer than tepals, 3–5-lobed. *Column* short and broad; anther-loculi parallel, canals absent; pollinia two, with short caudicles and round viscidia; lateral appendages present, longer or shorter than the anther; stigmas ± club-shaped, erect; rostellum short. *Capsules* erect, ellipsoid or cylindrical. **(PC)**

Distribution (Fig. 102.2)

A genus of four species in tropical and South Africa. **(PC)**

Palynology

Pollen sculpturing of *S. longifolia* is reticulate-heterobrochate. The foot-layer is verrucose (Schill and Pfeiffer 1977). **(AP)**

Cytogenetics

In the genus *Stenoglottis* the basic number is x = 18. Tanaka (1964) reported $2n = 2x = 36$ for *S. longifolia* Lindl. **(SD)**

Ecology

Stenoglottis plants usually occur on moss-covered boulders in forests or in sheltered rock crevices in cliffs, but they are occasionally epiphytic on trees (Schelpe 1966). *Stenoglottis zambesiaca*, for example, is principally found growing in submontane evergreen forests in southern Africa but also occasionally in woodland, on rotting logs, mossy rocks, and tree trunks (la Croix and Cribb 1995). This species occurs relatively high, from 1300–2150 m. Other species grow at lower elevations, e.g. *S. woodii* Schltr., up to 1500 m (la Croix and Cribb 1995).

Some *Stenoglottis* species have restricted ranges. *Stenoglottis longifolia* Hook.f. is confined to just a few localities in Zululand, and *S. woodii* has a scattered distribution across Transkei and Natal (S. Africa) and in Zimbabwe. The most common species is *S. fimbriata* Lindl., which is widely distributed through the forests of the eastern Cape Province, the Natal Midlands, and the Transvaal Drakensberg (Schelpe 1966).

Stenoglottis flowers between March and May, having been dormant over the winter, following a period of growth in the summer (Schelpe 1966). Fruit-set in *S. fimbriata* and *S. woodii* is presumably high; their flowers are reported to be consistently self-pollinating due to pollen germination of the undisturbed pollinia *in situ* and pollen tube growth from the anther sacs to the stigma (Schelpe 1966). **(RN)**

Uses

Stenoglottis are tolerant of pot cultivation. Three species are commonly found in cultivation, the finest being the South African *S. longifolia*, which can make fine specimen plants. **(PC)**

Cultivation

Stenoglottis has a long history in cultivation, needing to rest after flowering. Compost A and B. **(CB)**

Taxonomic notes

Stenoglottis is a distinctive genus, which was recently revised by Stewart (1989).

Taxonomic literature

Stewart, J. (1989). *Stenoglottis. Kew Magazine* **6** (1), 9–22.

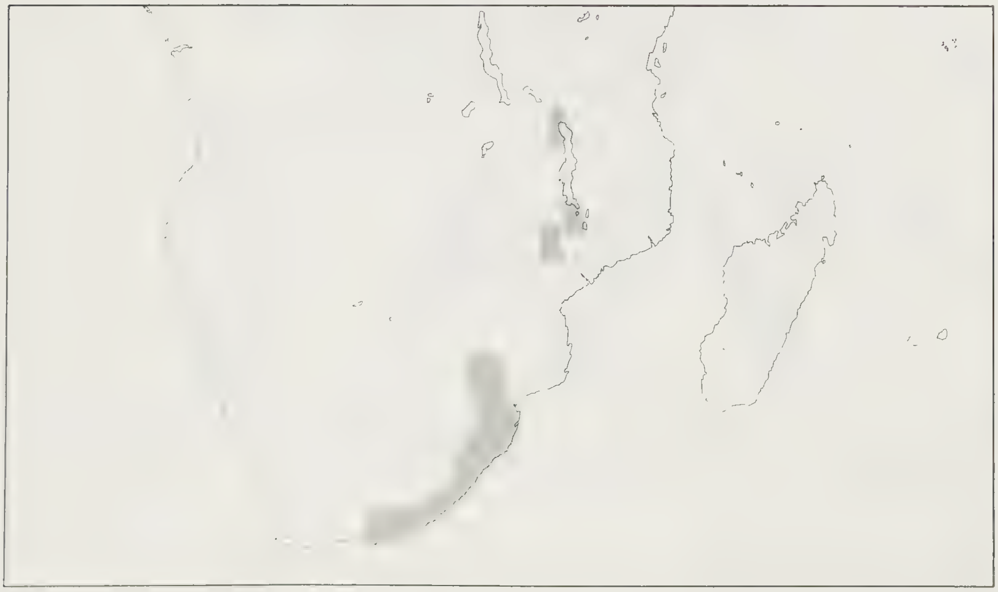

Fig. 102.2. Distribution map of *Stenoglottis.*

103. STEVENIELLA

Steveniella Schltr., *Feddes Repert.*, **15**, 293 (1918); Type species: *Steveniella satyrioides* (Spreng.) Schltr.

Stevenorchis Wankow & Kränzl., *Feddes Repert.*, **65**, 45 (1931). Type species: *Stevenorchis satyrioides* (Spreng.) Schltr. (= *Steveniella satyrioides* (Spreng.) Schltr.)

Derivation of name

Dedicated to Christian von Steven (1781–1863), the discoverer of the genus, who made many collections in the Caucasus during the early 19th century, and the Latin diminutive suffix *-ella*. **(JW)**

Description (Plate 120; Fig. 103.2)

Small to medium-sized *herbs*. *Rootstock* tuberous, tubers sessile. *Stem* erect, scapose, bearing two clasping sheaths. *Leaves* solitary, ligulate, often bent outwards, dark olive-green, longitudinally striped above with brownish purple, flushed beneath with purple. *Inflorescence* narrowly cylindrical, loosely many-flowered; floral bracts much shorter than ovary. *Flowers* adpressed to rachis, sepals dusty greenish purple outside, greyish purple spotted within, lip olive- or yellowish green, flushed purple toward base. *Sepals* and *petals* connivent, forming a closed hood, tips free. *Labellum* ligulate, with small rounded side lobes, bent toward ovary, spurred, spur adpressed to ovary, broadly conical, apex usually distinctly biconical. *Column* short, erect; pollinia two, each attached by a short caudicle to a viscidium, both viscidia enclosed in a solitary bursicle. **(JW)**

Distribution (Fig. 103.1)

A monospecific genus distributed in Turkey, the Crimea, the Caucasus, and northern Iran. **(JW)**

Palynology

Pollen sculpturing is approximately hamulate in *S. satyrioides* (Schill and Pfeiffer 1977). **(AP)**

Ecology

Steveniella grows on calcareous to neutral soils that are dry to damp and can tolerate conditions of full sun to semi-shade (Delforge 1995). It is usually found at high elevations, up to 2000 m, in a range of mountain habitats including open coniferous and deciduous woodlands, pastures and marshes, and nut-orchards. In the Crimean peninsula, *Steveniella* grows in forests in the mountains, usually on south-facing grass or moss-covered slopes (Nazarov 1995). It reportedly grew in relatively large colonies in this area in the past, especially where there was a well-developed moss cover and high surface-moisture content (Vanykov 1914, cited in Nazarov 1995), but it is now considered rare and listed in the Red Data Book of the Ukraine SSR and USSR (Nazarov 1995). It can still be found in quite large populations at some restricted localities throughout its range (Davies *et al.* 1988). Given that it is a nectarless orchid, fruit-set is high in this genus (Neiland and Wilcock 1998), for example 69% of flowers of *S. satyroides* set fruit in one population surveyed in the Crimean mountains in 1992 (Nazarov 1995). Unlike other orchids in the region growing in hornbeam-oak forest, which can suffer quite high levels of damage to their fruits (up to 43%) from the larvae of the tortrix moth (*Lobesia crimea*), insect), damage to *Steveniella* is insignificant (<1%). This form of herbivory does not appear to threaten the reproductive output of *Steveniella* in the Crimea at least (Nazarov 1987). **(RN)**

Pollination

The monospecific genus *Steveniella* has brownish green flowers with a short, bifid spur that contains no nectar (Nazarov 1995). Nazarov (1995) found two wasp species (*Paravespula vulgaris* and *Dolichovespula sylvestris*) as regular pollinators and suggested that *S. satyrioides* attracts these wasps with the help of the reddish brown papillae on the base of the lip and the spur entrance. Wasps are attracted to the reddish brown centre of the flower, which they seem to confuse with a piece of animal prey. Scratches from mandibles were commonly found on the inner surface of the spur. Nazarov (1995) suggested the term 'false-prey' syndrome for the pollination of *S. satyrioides*. **(AW, SC, AD)**

Uses

Tubers of *Steveniella* are probably collected in Turkey for the production of salep. **(JW)**

Cultivation

Steveniella grows in mountain pastures and open woodland. In the rare event that propagated plants are available, pot in compost C. **(CB)**

Taxonomic notes

Recent data from ribosomal DNA ITS sequences (Pridgeon *et al.*, unpublished) place *Steveniella* in the clade comprising *Barlia, Himantoglossum,* and *Comperia*. **(JW)**

Taxonomic literature

Delforge, P. (1995). *Orchids of Britain and Europe*. HarperCollins, London.

Taubenheim, G. (1980). Die Verbreitung der Orchideen in der Turkei IV/2. *Orchidee*, **31**, 5–10.

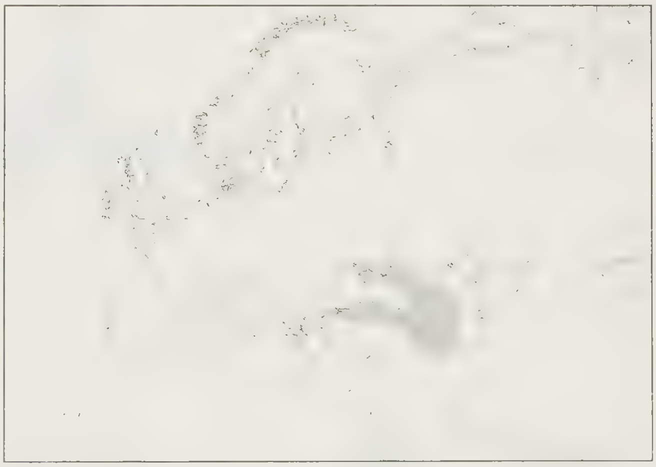

Fig. 103.1. Distribution map of *Steveniella*.

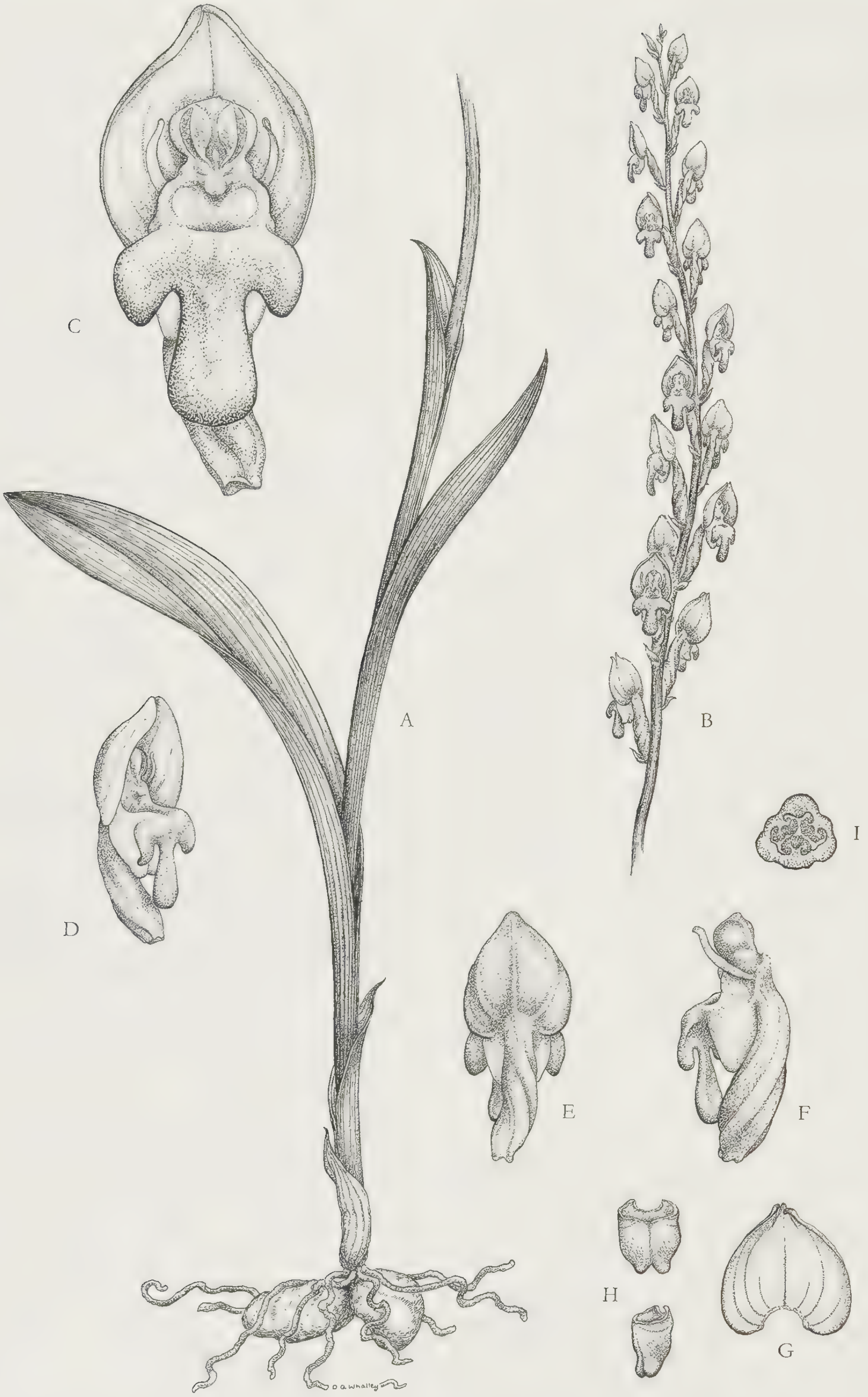

Fig. 103.2. *Steveniella satyrioides* (Spreng.) Schltr. A. Habit, ×1; B. Inflorescence, ×1; C. Flower from front, ×6; D. Flower, oblique view, ×3; E. Flower from behind, ×3; F. Flower, oblique view (sepals removed), ×3; G. Dorsal sepal, ×3; H. Spur from front and side, ×3; I. Ovary, transverse section, ×6. Drawn by Oliver Q. Whalley from Kew Spirit Collection no. 37051.

104. SYMPHYOSEPALUM

Symphyosepalum Hand.-Mazz., *Symbolae Sinicae*, **7**, 1327 (1936).
Type species: *Symphyosepalum gymnadenioides* Hand.-Mazz.

Derivation of name

From the Greek *symphyein*, grow together, and Latin *sepalum*, sepal, in reference to the sepals, which are connate for a third of their length. **(JW)**

Description (Fig. 104.2)

Perennial sympodial *herbs*. *Rootstock* tuberous, tubers subglobose, 0.5–1 cm in diameter. *Stem* 10–13 cm high, erect, angular, with scale-like cataphylls at base. *Leaves* two, grouped above base, elliptic-lanceolate, acute to acuminate, unspotted. *Inflorescence* densely many-flowered, erect; peduncle with a leafy bract; rachis 3–5 cm long; floral bracts leafy, long-acuminate, margin minutely papillose-ciliate, lowermost longer than flowers. *Flowers* resupinate, colour not noted, but probably white or pink. *Sepals* connate for a third of their length, 5 mm long, acuminate. *Petals* free, linear-lanceolate, acute, slightly shorter than sepals, 1 mm wide. *Labellum* spurred, porrect to deflexed, three-lobed, about 4 mm long, papillose, lobes obtuse, median longer than lateral, spur narrowly conical to cylindrical, obtuse, approximately 4 mm long, pendulous, with a somewhat horseshoe-shaped swelling at the entrance. *Column* short and broad; rostellum prominent, forming a narrow projecting roof; anther elliptic, erect, loculi parallel; pollinia not seen; a solitary bursicle possibly present. *Ovary* sessile. **(JW)**

Distribution (Fig. 104.1)

A monospecific genus distributed in south-western China. **(JW)**

Ecology

Symphyosepalum is recorded from bamboo forest on calcareous substrates between 3600–3900 m. **(JW)**

Uses

None recorded. **(JW)**

Cultivation

Unknown in cultivation. Compost C. **(CB)**

Taxonomic notes

This curious species is distinguished by the sepals that are connate for a third of their length and a labellum with a horseshoe-shaped swelling at the spur entrance. Living material is needed for its generic affinities to be clarified. **(JW)**

Taxonomic literature

Brieger, F. G., Maatsch, R., and Senghas, K. (1973). 36. *Symphyosepalum*. In *Rudolf Schlechter: Die Orchideen 3. Völlig neubearbeitete auflage* (ed. F. G. Brieger, R. Maatsch, K. Senghas), **4**, 235.

Handel-Mazzetti, H. (1936). *Symbolae Sinicae*; botanische ergebnisse der expedition der akademie der wissenschaften in Wien nach südwest-China 1914/1918. **7.** *Anthophyta*: 1327–8.

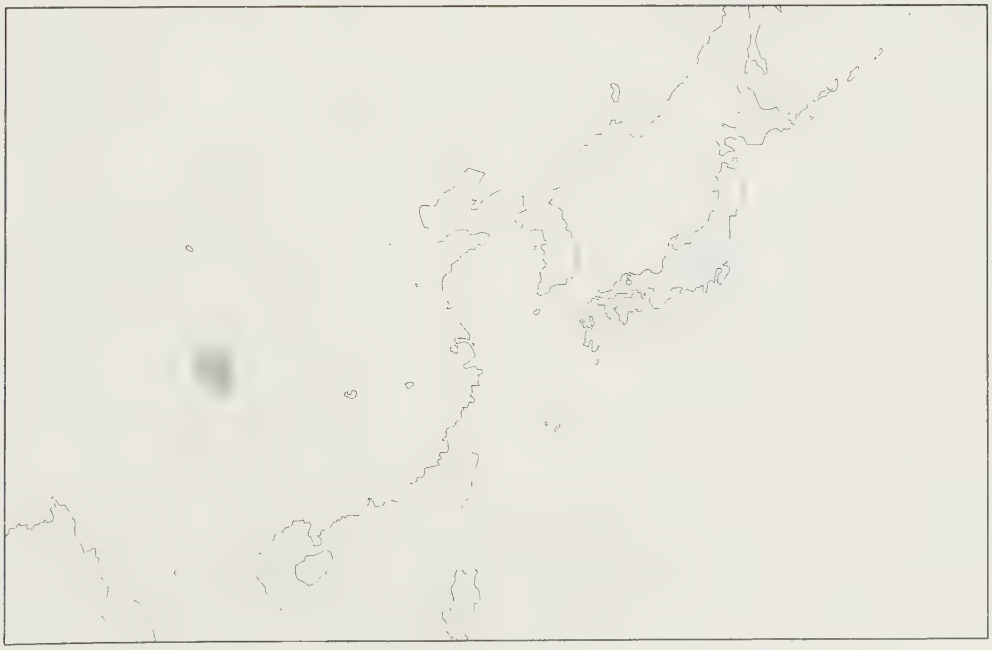

Fig. 104.1. Distribution map of *Symphyosepalum*.

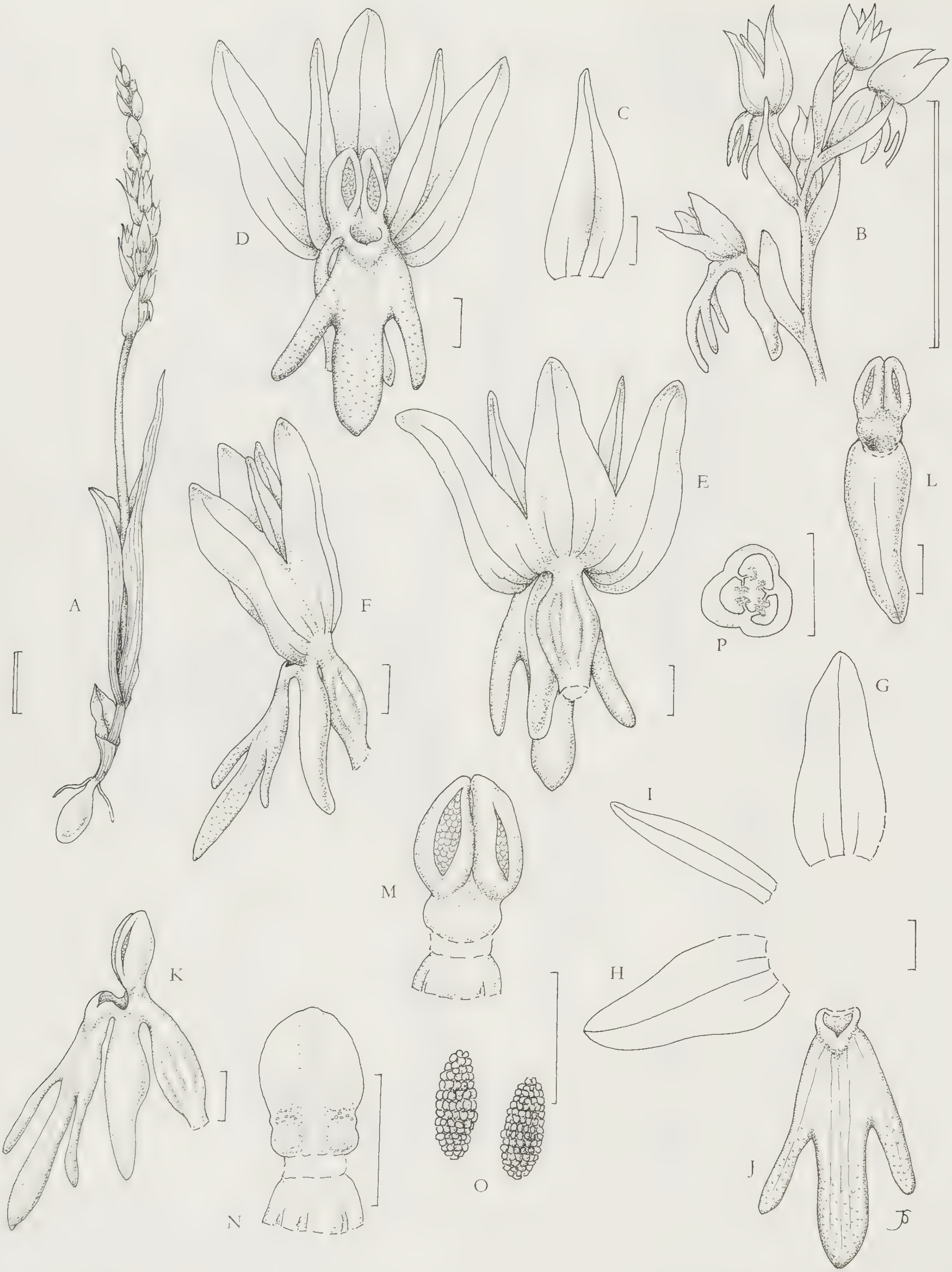

Fig. 104.2. *Symphyosepalum gymnadenioides* Hand.-Mazz. A. Habit; B. Inflorescence; C. Bract; D. Flower, front view; E. Flower, back view; F. Flower, side view; G. Dorsal sepal; H. Lateral sepal; I. Labellum; K. Labellum, spur, and column, side view; L. Spur and column, front view (lip removed); M. Column, front view; N. Column, back view; O. Pollinia; P. Ovary, transverse section. Single bar = 1 mm; double bar = 1 cm. Drawn by Judi Stone from *Handel-Mazzetti 5499* (holotype).

105. THULINIA

Thulinia P. J. Cribb, *Kew Bull.*, **40**, 401 (1985). Type species: *T. albolutea* P. J. Cribb

Derivation of name

Named after the Swedish botanist, Mats Thulin, who collected the type material. **(PC)**

Description (Plate 121; Fig. 105.2)

Terrestrial erect or subpendulous *herbs* arising from an ovoid pubescent tuber. *Leaves* 5–8, spreading-recurved, spirally arranged in basal half of stem, lanceolate, acuminate, the lowermost two reduced to sheaths. *Inflorescence* erect-flexuose, few-flowered; peduncle wiry; bracts lanceolate. *Flowers* glabrous, resupinate in a pendent raceme. *Sepals* not spreading widely, free, subsimilar. *Petals* free, similar but slightly shorter. *Labellum* much larger than the other perianth parts, flabellate, deeply emarginate with a basal cylindrical spur adnate to the ovary; callus verruculose. *Column* erect; anther loculi parallel; pollinia two, granular, clavate; viscidia two, small; stigmas short, oblong, papillose; rostellum obscure. **(PC)**

Distribution (Fig. 105.1)

A monospecific genus confined to the Nguru Mountains of eastern Tanzania. **(PC)**

Ecology

The Tanzanian endemic *T. albo-lutea* grows in montane grassland in the Nguru Mountains where it occurs on steep rocky slopes near the summit with other orchids such as *Neobenthamia gracilis* Rolfe and the endemic *Polystachya canaliculata* Summerh. *Thulinia albo-lutea* flowers in June (Cribb and Stewart 1985). **(RN)**

Uses

None recorded. **(PC)**

Cultivation

Compost C. **(CB)**

Taxonomic notes

Thulinia is allied to *Cynorkis* but distinguished by its marked callus on the lip and the spur, which is fused to the ovary. The inflorescence has a slender weak peduncle and may arch so that the lip lies lowermost. **(PC)**

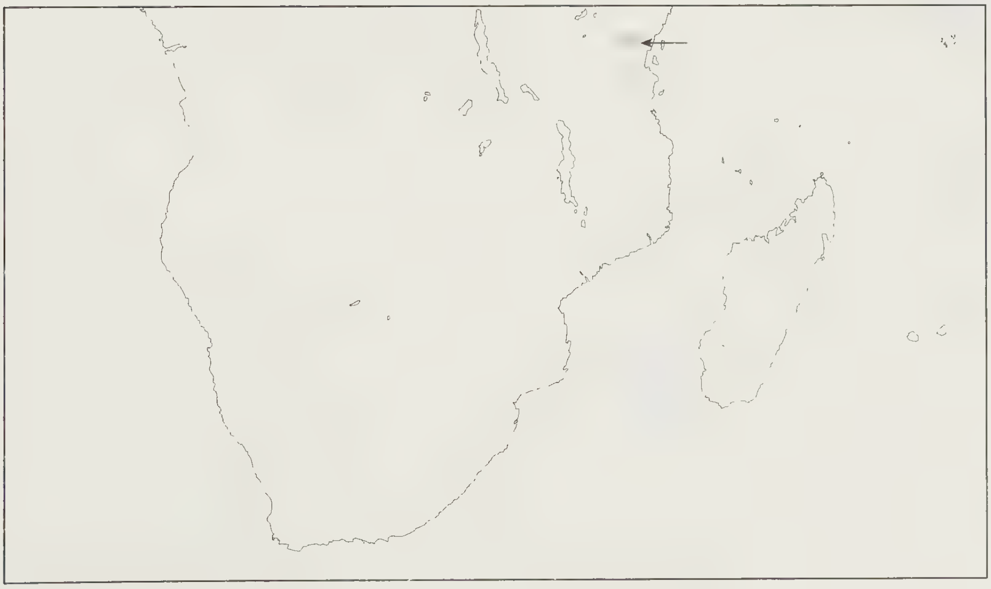

Fig. 105.1. Distribution map of *Thulinia.*

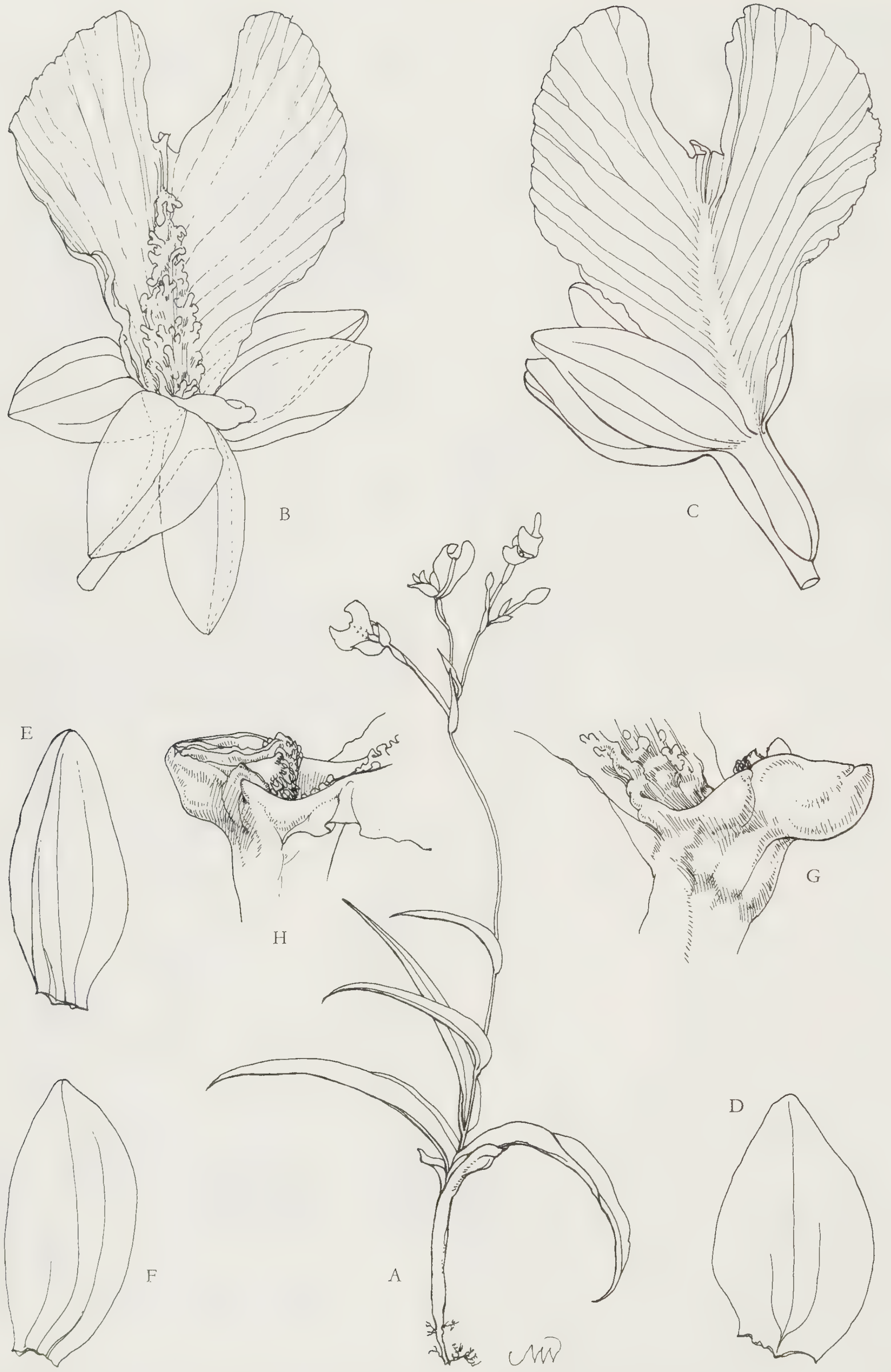

Fig. 105.2. *Thulinia albolutea* P. J. Cribb. A. Habit, ×1; B. Flower, front view, ×7; C. Flower, back view, ×7; D. Petal, ×9; E. Dorsal sepal, ×9; F. Lateral sepal, ×9; G. Column, oblique front view (magnification unspecified). H. Column, oblique back view (magnification unspecified). Drawn by M. Watt from *Thulin & Mhoro 3060.*

106. TRAUNSTEINERA

Traunsteinera Rchb., *Fl. Saxon.*, 87 (1842); Taubenheim, *Orchidee*, **30**, 223–8 (1979). Type species: *Traunsteinera globosa* (L.) Rchb.

Orchites Schur, *Enum. Pl. Transs.*, 942 (1866). Type species: *Orchites globosa* (L.) Schur. (= *Traunsteinera globosa* (L.) Rchb.)

Derivation of name

Honouring Josef Traunsteiner (1798–1850), an Austrian apothecary and botanist. **(JW)**

Description (Plate 122; Fig. 106.2)

Rootstock tuberous, tubers ovoid, entire. *Stem* erect, glabrous. *Leaves* two or three, oblong-lanceolate, remote, glaucous, unspotted, cauline only. *Inflorescence* densely many-flowered, globose or ovoid-spherical. *Flowers* small, rose-pink to purplish, or creamy white. *Dorsal sepal* and *petals* forming a loose hood. Sepals long acuminate, tips spathulate. *Labellum* three-lobed, shortly spurred. *Column* short, obtuse; rostellum three-lobed, median lobe erect, linear, tip hooded; pollinia two, attached to separate viscidia partly enclosed in a slightly bipartite, rudimentary bursicle. *Ovary* cylindrical, sessile, slightly twisted, glabrous. **(JW)**

Distribution (Fig. 106.1)

A genus of two species only. *Traunsteinera globosa* is distributed in the hilly and mountainous regions of western, central, and south-eastern Europe south to Italy and east to Poland. *Traunsteinera sphaerica* Schltr. occurs in Turkey and the Caucasus. **(JW)**

Ecology

Traunsteinera is typically found in the sub-alpine zone of mountainous areas at elevations above 1500 m (range 1000–3000 m; Davies *et al.* 1988). It grows in slightly acid to alkaline soils, which may be dry to damp, and occurs in a range of habitats including poor grassland, alpine meadows, highland marshes, and open coniferous woodlands, but always in full sunlight. The co-occurring grassland vegetation is often relatively tall (Davies *et al.* 1988). Flowering plants co-occurring with *T. globosa* in northern Italy include *Scabiosa columbaria* L. (Dipsacaceae) at low elevations and *Valeriana montana* L. (Valerianaceae) at high elevations, both of which closely resemble the appearance of the orchid. It has been suggested that *T. globosa* mimics these and other species to attract insect pollinators (Dafni 1987).

The flowering period of *Traunsteinera* populations is sometime between May and August, depending on elevation. As the individual flowers open, the dense globose or pyramidal inflorescence elongates (Davies *et al.* 1988). Seeds have been collected from *T. globosa* and germinated asymbiotically in culture within three months (Veyret 1969). *Traunsteinera* perennates by means of a relatively small tuber and has long, thick roots (Fuchs and Ziegenspeck 1925, cited in Rasmussen 1995).

Traunsteinera is recorded as locally rare in parts of its distribution. Delforge (1995) noted that it is particularly rare in the eastern part of its range in Anatolia (Turkey). **(RN)**

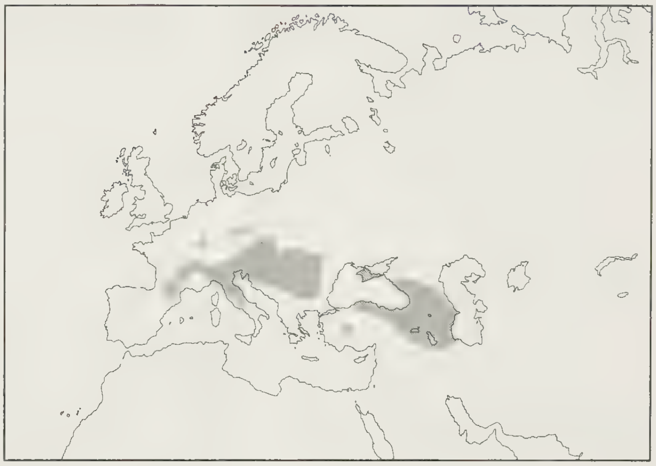

Fig. 106.1. Distribution map of *Traunsteinera.*

Pollination

Traunsteinera globosa is visited by a wide variety of insects. Hoverflies, bees, butterflies, and beetles were observed visiting the flowers (Dafni 1987; Reinhard *et al.* 1991; Vöth 1994), but it remains to be established which are effective pollinators and which are unable to remove pollinaria or do so only rarely. Dafni (1987) suggested that *T. globosa* mimics *Scabiosa columbaria* (Dipsacaceae), with which it shares habitat and which has a similar appearance. **(AW, SC, AD)**

Uses

None recorded. **(JW)**

Cultivation

Both species grow in calcareous alpine meadows. Use compost C with added lime. **(CB)**

Taxonomic literature

Taubenheim, G. (1979). Verbreitung der Orchideen in der Türkei IV/I. *Orchidee*, **30**, 223–8.

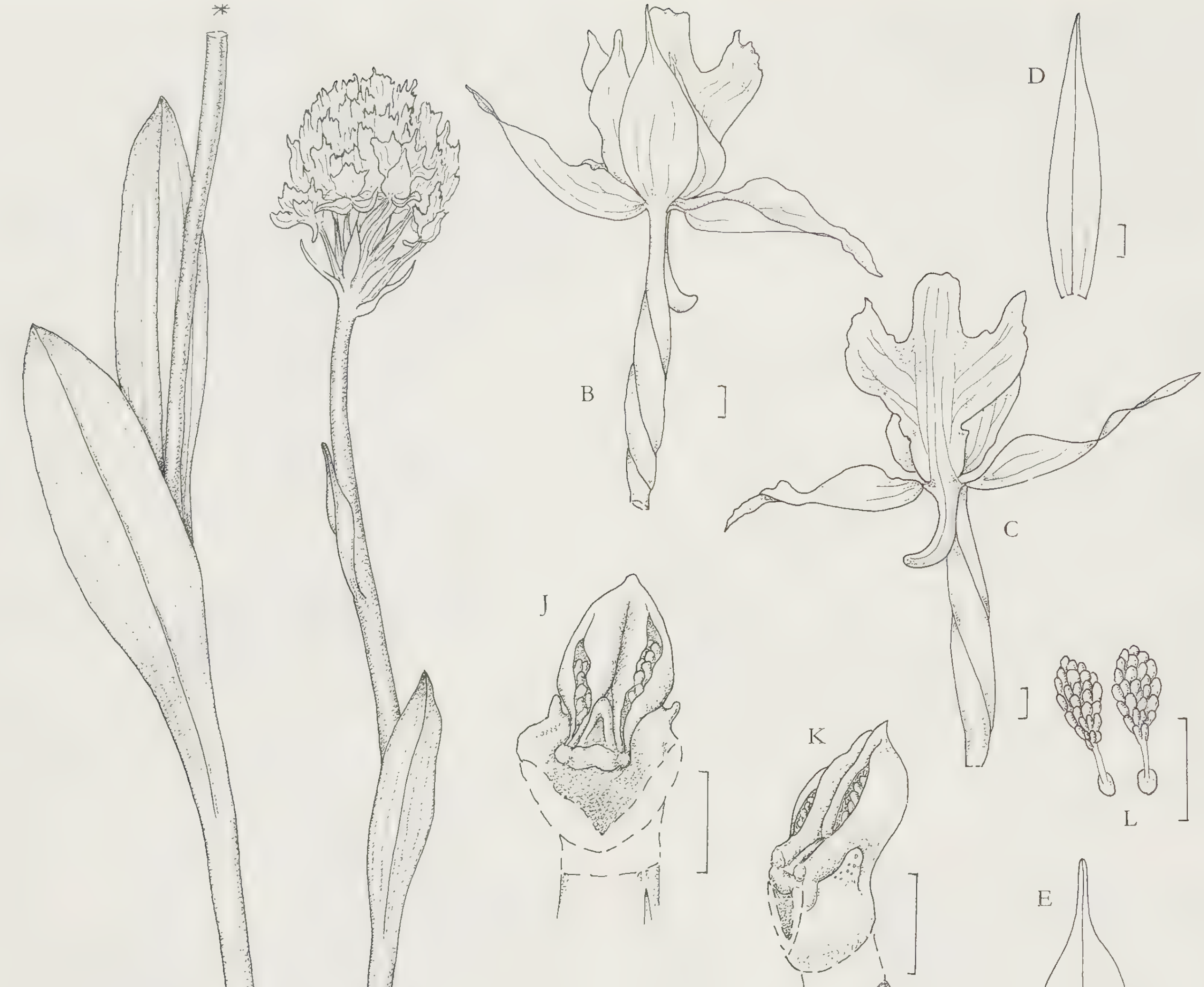

Fig. 106.2. *Traunsteinera globosa* (L.) Rchb. A. Habit; B. Flower, back view; C. Flower, front view; D. Bract; E. Dorsal sepal; F. Lateral sepal; G. Petal; H. Labellum; I. Labellum and column, side view; J. Column, front view; K. Column, side view; L. Pollinaria; M. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Thure s.n.* and Kew Spirit Collection no. 40611.

107. TYLOSTIGMA

Tylostigma Schltr., *Beih. Bot. Centralbl.*, **4**, 298 (1916). Type species: *T. madagascariensis* Schltr. (lectotype, chosen here).

Derivation of name

From the Greek *tylos*, a knob, and *stigma*, a stigma, probably in reference to the stigma shape. **(PC)**

Description (Fig. 107.2)

Perennial, glabrous *herbs* with fleshy tuberous roots. *Stems* slender, straight, bare or unifoliate at the base, or bearing a few leaves in the middle. *Leaves* suberect, fleshy, narrowly linear, acute. *Inflorescence* racemose, elongate, narrow, sparsely to subdensely many-flowered. *Flowers* small, glabrous. *Sepals* and *petals* slightly connivent. Sepals free, ovate or oblong, obtuse, the laterals somewhat oblique. *Petals* obliquely oblong or suborbicular, obtuse, a little smaller than the sepals. *Labellum* sessile, subcordate at the base, fleshy, entire, glabrous, ovate, obtuse, as long as or longer than the petals, ecalcarate with a transverse lamellate callus at the base, variously ornate in front. *Column* short, stigma sessile, pulvinate, only slightly bilobed; rostellum trilobed, obscure; lateral appendages short; anther erect, coronate; anther loculi parallel, lacking canals; pollinia pyriform, granular; viscidia two, distinct, orbicular. **(PC)**

Distribution (Fig. 107.1)

A small genus of seven species endemic to Madagascar. **(PC)**

Ecology

Most species of the Madagascan endemic genus *Tylostigma* are terrestrial orchids growing in the wet, peaty soil of marshland. Exceptions are *T. tenellum* Schltr., which is a lithophyte, and the terrestrial species, *T. nigrescens* Schltr., which is recorded from a cypress plantation (Du Puy *et al.* 1999). *Tylostigma* grows at elevations between 1400 and 2500 m. Most species flower between December and March, although *T. tenellum* flowers in May and *T. perrieri* Schltr. between April and July (Du Puy *et al.* 1999). Like other orchids on the island, *Tylostigma* is threatened by habitat loss and degradation, and J. M. Bosser (IUCN Orchid Specialist Group 1996) listed it as a priority taxon for conservation action. **(RN)**

Uses

None recorded. **(PC)**

Cultivation

Compost A or B. **(CB)**

Taxonomic notes

The most recent account of the genus was given by Perrier de la Bâthie (1939). An updated nomenclature was provided by Du Puy *et al.* (1999).

Taxonomic literature

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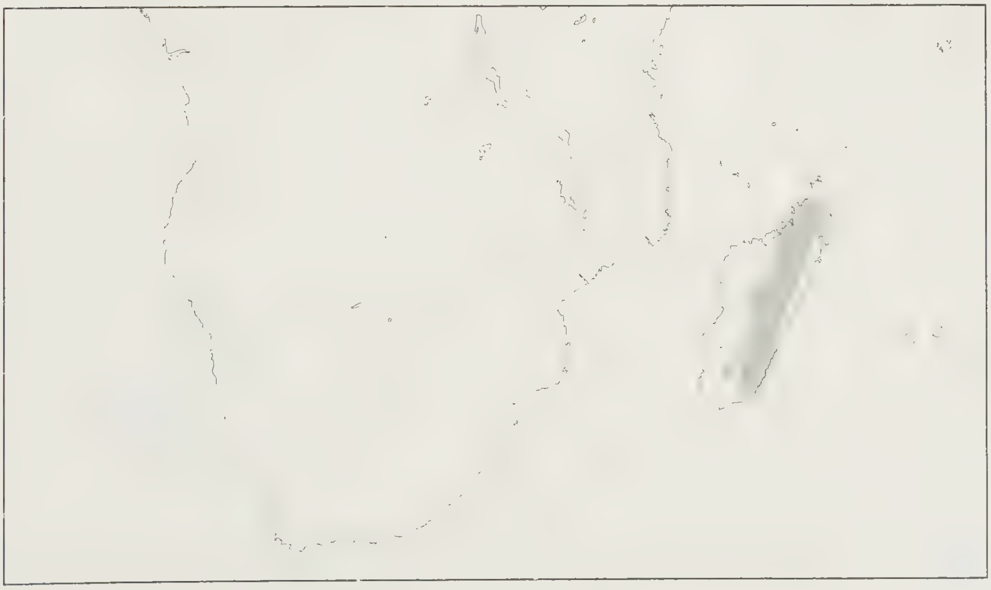

Fig. 107.1. Distribution map of *Tylostigma.*

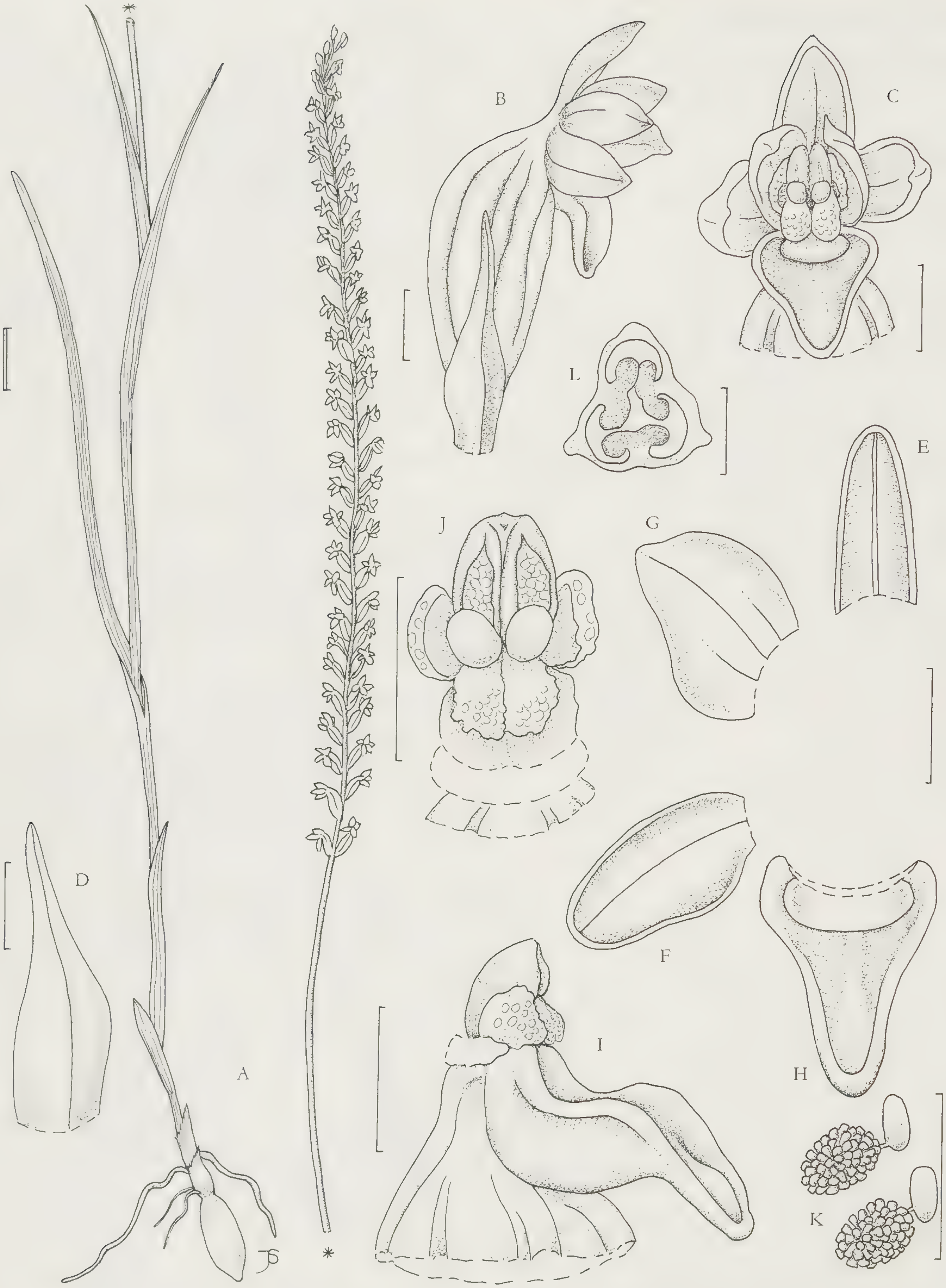

Fig. 107.2. *Tylostigma hildebrandtii* Schltr. A. Habit; B. Flower, side view; C. Flower, front view; D. Bract; E. Dorsal sepal; F. Lateral sepal; G. Petal; H. Labellum; I. Labellum and column, side view; J. Column, front view; K. Pollinaria; L. Ovary, transection. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Baron 6750*.

108. VEYRETELLA

Veyretella Szlach. & Olsz., *Fl. Cameroun Orchidacées*, **1**, 100 (1998). Type species: *V. hetaerioides* (Summerh.) Szlach. & Olsz. (basionym *Habenaria hetaerioides* Summerh.).

Derivation of name

Named for Dr Yvonne Veyret, the French botanist and orchid expert. **(PC)**

Description (Fig. 108.2)

Glabrous, terrestrial *herbs* with elongate rhizomes and fleshy roots. *Stem* erect, leafy. *Leaves* several, cauline. *Inflorescence* terminal, several-flowered, racemose, glabrous; bracts leaf-like. *Flowers* resupinate, white, glabrous; pedicel and ovary glabrous. *Sepals* free, the lateral sepals oblique, spreading. *Petals* linear, one-veined. *Labellum* three-lobed, with a fleshy basal callus, spurred at the base; side lobes small, spreading, lacerate; mid-lobe flabellate; spur elongate, tapering to base. *Column* short and broad; androclinium erect; anther loculi parallel, the canals long and slender; viscidia two, lateral appendages distinct; stigmatic processes shortly clavate; side lobes of rostellum elongated; mid-lobe large, projecting forward. *Capsules* unknown. **(PC)**

Distribution (Fig. 108.1)

A monospecific genus endemic to Gabon. **(PC)**

Uses

None recorded. **(PC)**

Taxonomic notes

Szlachetko and Olszewski (1998) established *Vereytella* for the aberrant Gabonese endemic *Habenaria hetaerioides* Summerh. which Szlachetko had earlier transferred to *Cynorkis*. Summerhayes (1938) had referred it to *Habenaria* sect. *Plantaginea*, but it is aberrant there because of its creeping rhizome; linear, one-veined petals; three-lobed lip with tridentate side lobes and a much larger flabellate mid-lobe; and a distinct basal callus. Likewise it is aberrant in *Cynorkis*. In fact, at first sight, it resembles a white-flowered *Brachycorythis*, but the column is distinct. We are therefore inclined to accept it as distinct at generic rank pending further work. **(PC)**

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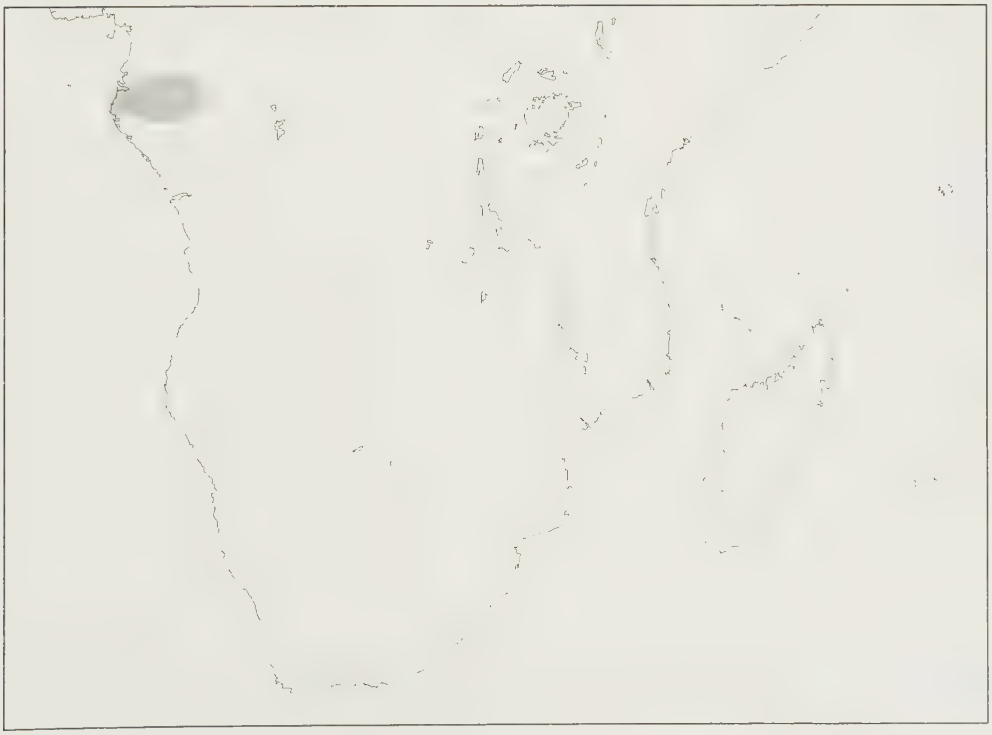

Fig. 108.1. Distribution map of *Veyretella*.

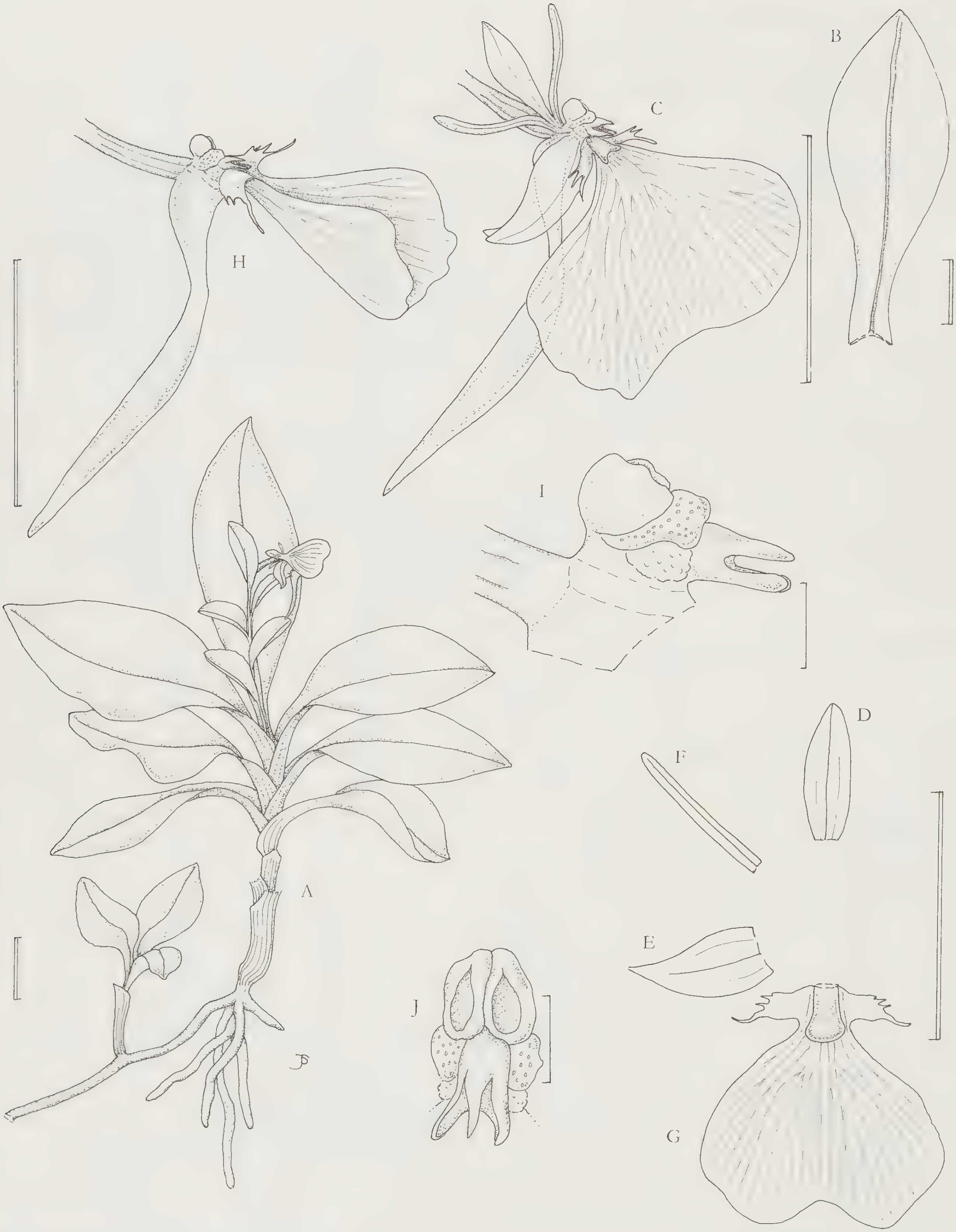

Fig. 108.2. *Veyretella hetaerioides* (Summerh.) Szlach. & Olszewski. A. Habit; B. Leaf; C. Flower; D. Dorsal sepal; E. Lateral sepal; F. Petal; G. Labellum; H. Labellum and column, side view; I. Column, side view; J. Column, front view. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Le Testu 2214*.

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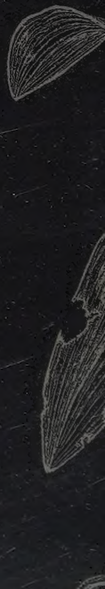

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